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Dendroid and Tuboid Graptolites from the Llandovery (Silurian) of the Four Mile Creek Area, New South Wales

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ABSTRACT. Twenty-four taxa of Llandovery (Early Silurian) dendroid and tuboid graptolites from the Cadia Coach Shale and Glendalough Formation in the Four Mile Creek area, S of Orange, New South Wales, provide the most diverse benthic graptolite record known from rocks of this age.

Eighteen new taxa described here are: the dendroids *Dendrograptus avonleaensis, D. ashburniaensis, Dictyonema williamsae, D. paululum australis, D. jenkinsi, D. muirae, D. warrisi, Callograptus bridgecreekensis, C. rigbyae, C. ulahensis, Stelechocladia praeattenuata, Acanthograptus praedeckeri, A. praedeckeri minimus, Thallograptus christoffersonae, Koremagraptus obscurus* and *C. elegantulus*; and the tuboids *Reticulograptus thomasi* and *Cyclograptus? australis*. The six previously-named taxa are: *Dictyonema* cf. *delicatulum* Lapworth, *D. falciferum* Bulman, *D. venustum* Lapworth, *Callograptus* cf. *niagarensis* Spencer and *Pseudodictyonema graptolithorum* (Počta); and one species in open nomenclature is *Dictyonema* sp. 1. These occur with graptoloids at Four Mile Creek, allowing precise stratigraphic correlation of the faunas with probably the *gregarius* Biozone (middle Llandovery), and the *crispus* and *griestoniensis* Biozones (late Llandovery) of Europe.

Criteria for dendroid classification are discussed and some implications for reconstructing the evolutionary history of the group are reviewed. The evolution of anastomosis and dissepiments is seen as of prime importance in the development of three major changes in the Middle to Late Cambrian, which are: 1, ordered *Dendrograptus* → *Callograptus*: 2, ordered *Dendrograptus* → *Dictyonema*; 3. ordered *Dendrograptus* → *Desmograptus*. The development of compound stipes, while important in defining the Acanthograptidae, is recognized as having arisen independently in three other lineages.

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Contents

Silurian graptolite faunas have been known from the Four Mile Creek (formerly known as Panuara Rivulet) area (Fig. 1) S of Orange (33°17'S 149°6'E), New South Wales, for 50 years (Stevens & Packham, 1953). These fossils are important in the global context as they give a basis for very fine correlation of Silurian strata; when these NSW faunas are fully documented, they will provide a framework for calibration of the geological evolution of this part of the eastern Lachlan Fold Belt. This is potentially important in view of the active gold exploration programmes in the region (see also Packham *et al.*, 1999). In the global context, these studies will shed more light on the evolution, palaeoecology and biogeography of graptolites. In addition, far-reaching tectonic and sea level interpretations (Jenkins, 1978; Packham, 1969) have been made on the basis of preliminary identifications of the faunas, and some of these interpretations have been quoted in global considerations of Silurian sea level changes (Johnson *et al.*, 1991; Johnson & McKerrow, 1991); there is an urgent need to describe and assess the present faunas fully to permit evaluation of these interpretations.

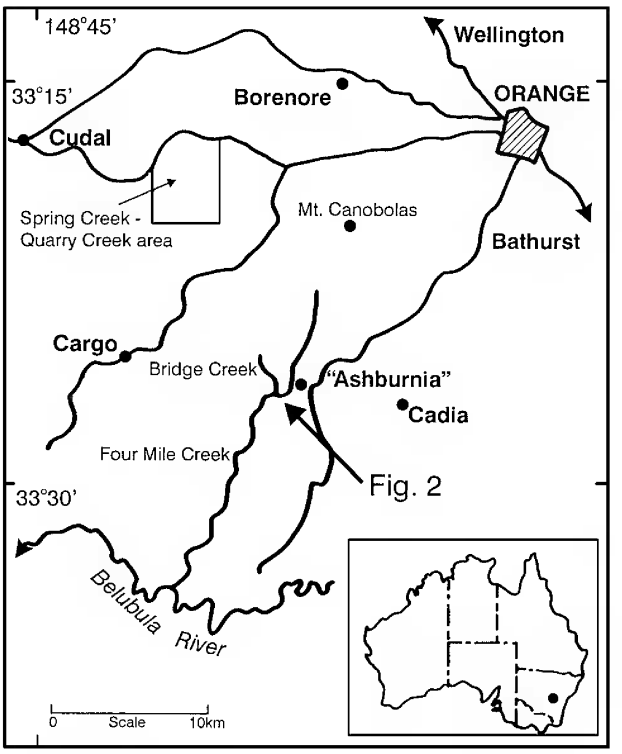

Fig. 1. Location map of the Bridge Creek area of southeastern Australia.

Previous studies of the area

Pioneering studies in the southern part of the area by Booker (1950) recognized a belt of limestone extending from the Belubula River in the S to Cobblers Creek in the N; Booker considered this Late Silurian, which is not supported by later studies. Carne & Jones (1919: 177–178) mentioned that limestone extended from (what is now known to be Ordovician) Cliefden Caves across the Belubula River into portion 3, parish Carlton, county Bathurst. Stevens & Packham (1953) greatly extended knowledge of the Ordovician and Silurian strata in the region and first interpreted the graptolite faunas of the area. Detailed mapping and palaeontological studies of the Four Mile Creek region were carried out by Warris (1964) and Jenkins (1973).

Graptolites previously described and illustrated from the Four Mile Creek area include the Llandovery species *Glyptograptus tamariscus, Monograptus triangulatus, Monograptus intermedius* and *Rastrites longispinus* described by Sherrard (1954: pl. XI, 99–100) and the Wenlock fauna described by Rickards & Wright (1997). Sherrard (1954: 90–91) listed several Llandovery faunas and one Wenlock graptolite fauna from the "Angullong" area S of the Bridge Creek area, and illustrated *Cyrtograptus* cf. *insectus* (Sherrard, 1954: 76, fig. 1.3) and *Monograptus exiguus, M. marri* and *M. dubius* (Sherrard, 1954, figs. 1.1, 1.4, and 1.5 respectively) from "Four Mile Creek". Apart from these very preliminary studies of the faunas, there remain rich and essentially undescribed Llandovery, Wenlock and Ludlow graptolite faunas in the area.

In addition to the prolific, diverse and well-preserved graptolites of the Llandovery to Ludlow of the Four Mile Creek area, important faunas are known elsewhere in the region from Spring and Quarry Creeks (Packham & Stevens, 1955; Rickards *et al.*, 1995), and from Cheesemans Creek (Sherwin, 1971); both areas are located N of the present study area (Fig. 1).

This paper is the first part of our investigation and interpretation of the Four Mile Creek faunas, biostratigraphy and sequences. We describe here by far the most diverse Llandovery dendroid graptolite fauna on record, being almost exclusively from several localities in the valley of Bridge Creek, a major tributary of Four Mile Creek (Figs. 1, 2).

Geological setting

Silurian strata discussed here occur south and west of the old settlement of Four Mile Creek in the gently undulating topography of the valley of Four Mile Creek; the most important outcrops are in or along Four Mile Creek, its tributaries Bulls Camp Creek and Bridge Creek, and (a tributary of the latter) Wallace Creek (Fig. 2). Silurian faunas have also been documented from strata east of Four Mile Creek in the vicinity of the Cadia Mine, in an area of predominantly Ordovician rocks (Offenberg, 1963; Rickards *et al.*, 2001).

The faunas described here are from the two lower groups of the three comprising the Silurian to basal Devonian succession in the Four Mile Creek area; these are, in ascending order, the Ashburnia, Waugoola and Mumbil Groups (Pogson & Watkins, 1998). Our collections are from strata exposed on the eastern limb of a syncline (Fig. 2); the west-dipping succession has been disrupted by faulting and is uncleaved; Cthe graptolite faunas are largely undeformed. In this area the Ashburnia and Waugoola

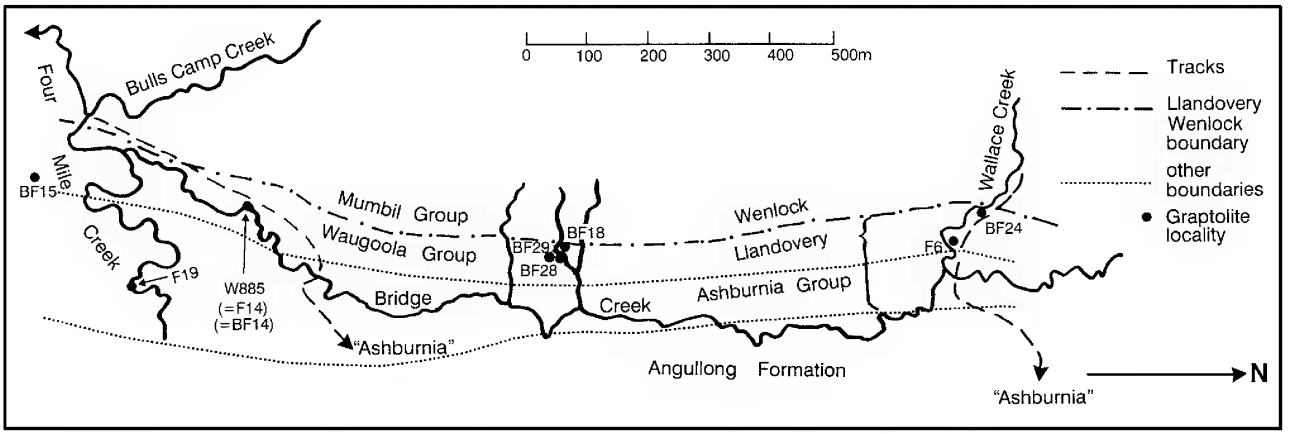

Fig. 2. Dendroid graptolite localities on the Bridge Creek sections.

Table 1. Lithostratigraphic units from the Four Mile Creek area, according to current terminology, which are mentioned in text; all named units are not shown. New faunal data and mapping indicate a hiatus above the *spiralis* bed, and the Burly Jacky Sandstone is placed in the Mumbil Group. Units that have yielded graptolites are in bold type.

MUMBIL GROUP (Wenlock-Pridoli)	Wallace Shale	
	Ulah Formation	higher beds Burly Jacky Sandstone Member
WAUGOOLA GROUP (late Llandovery)	**Glendalough Formation**	***spiralis* beds** (*griestoniensis* Biozone) ***exiguus* bed** (*crispus* Biozone)
ASHBURNIA GROUP (early to middle Llandovery)	**Cadia Coach Shale**	**Avon Lea Mudstone Member** (*gregarius* Biozone)
	Bagdad Formation	

Groups are about 80 and 60 m thick respectively, consisting of calcareous and clastic sediments. There is an erosional break or unconformity between the Ashburnia Group and the underlying Late Ordovician volcanic Angullong Formation. The Silurian strata are overlain unconformably by gently folded Late Devonian sandstone, conglomerate and shale forming timbered ridges almost exclusively located on the W side of Four Mile Creek.

The Silurian lithostratigraphic sequence in the area has been described in detail by Jenkins (1973, 1978, 1986) and Pogson & Watkins (1998), and is summarized in Table 1. From our preliminary reassessment of the faunas and field studies (both here and at Spring-Quarry Creek: see Fig. 1) it seems likely that changes will be necessary to the stratigraphic terminology and relationships, and age assignments. For instance, our studies indicate that the Burly Jacky Sandstone Member and overlying strata placed by Jenkins (1978) in the Waugoola Group should be recognized as part of the Mumbil Group (Table 1). Nevertheless, the stratigraphic position of the present faunas from in the immediate vicinity of Bridge Creek (Fig. 2) is very clear and, based on our preliminary study of the associated graptoloids, we agree broadly with age assignments made for these dendroid faunas by Jenkins (1978).

The oldest Silurian unit in the area is the early to middle Llandovery Ashburnia Group, a name introduced by Pogson & Watkins (1998) to replace the Cadia Group of Jenkins (1978). The basal Bagdad Formation of clastics and limestones, which includes the Bridge Creek Limestone Member, is overlain by the Cadia Coach Shale. At the base of the latter formation is the Avon Lea Mudstone Member; locality F19 is located in this unit, and is provisionally assigned by us to the uppermost *gregarius* Biozone of middle Llandovery age. The only dendroid species from this locality is *Stelechocladia praeattenuata* n.sp., also known from higher localities. All other localities discussed herein are from the overlying Waugoola Group.

The late Llandovery Waugoola Group is represented in the area in Fig. 2 by the Glendalough Formation. Jenkins (1978, 1986) divided the lower shaly part of the formation into two units; siliceous sandy shale in the lower part which he termed the "*exiguus* bed" and the upper olive green shaly unit which he called the "*spiralis* beds". Localities BF15 and F6 in the "*exiguus* bed" are within the *crispus* Biozone (of late Llandovery age). In the lower part of the "*spiralis* beds", locality BF14 (= W885 and F14) is in the lower part of the *griestoniensis* Biozone and localities BF 28, BF 29, BF24 and BF18 are from the upper part of the "*spiralis* beds" and have been correlated with the upper *griestoniensis* Biozone (also of late Llandovery age). The last mentioned locality (BF18) is in the highest beds of the "*spiralis* beds" where the shales are more siliceous and thin bands of lithic sandstone are interbedded; *Stomatograptus grandis* is also present at this level.

Faunal assemblages

The faunas discussed here have been collected from eight localities, one of which (F14=BF14=W885) has produced by far the largest assemblage of 18 species (Table 2). At this locality dendroids outnumber graptoloids in both diversity and abundance. F19 is located within the Avon Lea Mudstone Member of the Cadia Coach Shale, Ashburnia Group; and all other localities are in the Ashburnia Group.

Comparison with other late Llandovery dendroid faunas

The late Llandovery has in many parts of the world well-preserved dendroid graptolite faunas, but none has the high diversity recognized at Four Mile Creek. Bulman's (1928) monograph on British dendroids, for example, listed only five species for the whole of Britain, and Bull (1987) recorded six species from rich and well-preserved dendroid faunas in the late Llandovery of Scotland. In his classic monograph on Czech dendroids, Bouček (1957) recorded only 6 species from the whole Llandovery; although this work has been supplemented by further records of a small number of species by Kraft (1979, 1984), only a few are from the late Llandovery. Ruedemann (1947) recorded over 70 dendroid taxa for the Silurian of North America, but proportionally fewer from the late Llandovery, and most of these are in low diversity assemblages. The most spectacularly diverse North American dendroid faunas are from the Lockport

Table 2. Stratigraphic distribution of dendroid graptolite taxa described in this paper (closed circle = presence). The oldest locality F19 (Avon Lea Mudstone Member, Cadia Coach Shale, Ashburnia Group) is at extreme left. All other, younger localities (Glendalough Formation, Waugoola Group) range from the lowest locality BF15 at the left, to the youngest locality BF18 at extreme right.

	F19	BF15	F6	F14	BF28	BF29	BF24	BF18
Dendrograptus avonleaensis n.sp.	○	○	○	●	○	○	○	○
Dendrograptus ashburniaensis n.sp.	○	○	○	●	○	○	○	○
Dictyonema jenkinsi n.sp.	○	○	○	●	○	○	○	○
Dictyonema muirae n.sp.	○	○	○	●	○	○	○	○
Dictyonema venustum	○	○	○	●	●	○	○	○
Dictyonema sp. 1	○	○	○	●	○	○	○	○
Dictyonema falciferum	○	○	○	●	○	○	○	○
Dictyonema cf. *delicatulum*	○	○	○	●	○	○	○	○
Dictyonema paululum australis n.sp.	○	○	○	●	○	○	○	○
Dictyonema williamsae n.sp.	○	○	○	●	○	○	○	○
Dictyonema warrisi n.sp.	○	○	○	●	○	○	○	○
Callograptus rigbyae n.sp.	○	○	○	●	●	○	○	○
Callograptus bridgecreekensis n.sp.	○	○	○	●	○	○	○	○
Callograptus cf. *niagarensis*	○	○	○	●	○	○	○	○
Callograptus ulahensis n.sp.	○	●	○	○	○	○	○	○
Pseudodictyonema graptolithorum	○	○	○	●	○	○	○	○
Stelechocladia praeattenuata n.sp.	●	○	○	○	●	○	●	●
Acanthograptus praedeckeri n.sp.	○	○	●	●	●	●	○	○
Acanthograptus p. minimus n.subsp.	○	○	●	○	○	○	○	○
Thallograptus christoffersonae n.sp.	○	○	○	●	●	●	○	○
Koremagraptus obscurus n.sp.	○	○	○	○	●	○	○	○
Koremagraptus elegantulus n.sp.	○	○	○	●	○	○	○	○
Reticulograptus thomasi n.sp.	○	○	○	○	●	○	○	○
Cyclograptus? australis n.sp.	○	○	○	○	●	○	○	○

dolomites and limestone (Ruedemann 1947, pp. 128–9) but these are of Wenlock/Ludlow age. Silurian dendroids are known from both Russia and China but no Llandovery horizons have been described with highly diverse dendroid faunas: for example Obut & Sobolevskaya (1966) recorded three dendroid species from the early Llandovery (and one species from the early Wenlock).

Preservation of the graptolites

There is no tectonic deformation of the graptolites. There is some crumpling of stipes during burial and diagenetic flattening, but this is usually infrequent and easily detected. A surprising number of specimens are more or less complete, some with holdfasts, or are large fragments, indicating that transport has been low: however, dendroid debris indicates that some transport has occurred so that the assemblages cannot be considered as biocoenoses. The rock type is mud to silt grade with occasional fine sand laminae, and some hemipelagic layers. In general the stipes are in low relief, the original (carbonized) periderm well-preserved, and there may be partial infills of mud or pyrites. Specimens in full relief, or fully infilled with pyrites have not been observed.

Classification of dendroid graptolites

The most recent attempt to arrange dendroids in a provisional classification was by Chapman *et al.* (1996). They noted that rhabdosomal form seemed of lesser importance in classification than the manner in which the stipes were connected, so that species of *Dictyonema* might be conical, cyathiform, or discoidal. However, the uniting feature of species of *Dictyonema* is the branching pattern and the stipe connections by numerous dissepiments. *Callograptus* can be conical or flabellate, is very similar, but has few or no dissepiments. In *Desmograptus* Hopkinson *in* Hopkinson & Lapworth, 1875, the stipes unite by anastomosis, as they do in *Polygonograptus* Bouček, 1957, but the bulk of the remaining genera exhibit *Dendrograptus* style of bushy branching (see Chapman *et al.*, 1996, figs. 2, 3). Some genera such as *Koremagraptus* exhibit a variety of stipe connections usually involving autothecal transfer from one stipe to another.

Stipe structure has some broad classificatory value in that the Acanthograptidae develop compound stipes, whereas most of the Dendrograptidae have relatively simple stipes. However, in the Dendrograptidae, *Callograptus* gave rise to the compound *Pseudocallograptus* Skevington, 1963, *Dictyonema* gave rise to *Pseudodictyonema* Bouček, 1957, and *Dendrograptus* gave rise to *Stelechocladia* Počta, 1894.

These classificatory features were placed in a stratigraphic context by Chapman *et al.* (1996; see Figs. 2, 3 herein). Thus the bushy dendroid habit is the earliest in the stratigraphic record, followed quickly by more regular branching patterns, then stipe connections through anastomosis and dissepiments, and the development of conical and other more ordered colonies (*Callograptus, Dictyonema* and *Desmograptus*).

Chapman *et al.* (1996) concluded that there was a morphological and stratigraphic series, beginning in the Middle Cambrian, from *Dendrograptus* (disordered and ordered) to *Callograptus, Dictyonema* and *Desmograptus*,

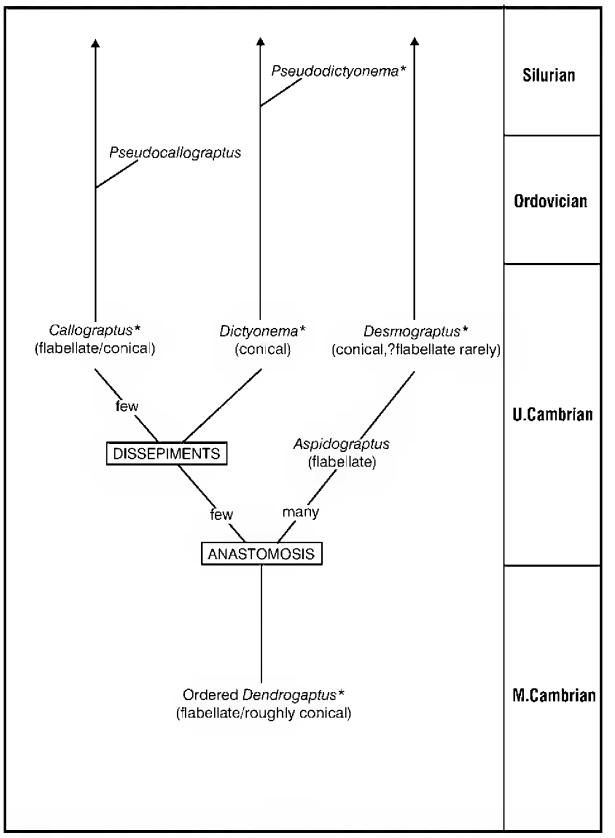

Fig. 3. Early evolution of some benthic Dendroidea, and modifying the suggestions of Chapman *et al.* (1996), and illustrating the rôle of anastomosis and dissepiments development. Full explanation is to be found in text. Asterisks indicate genera from which species are described in this paper. Boxes indicate approximate time of appearance of that character.

and that this supported the use of rhabdosomal stipe connection (but not gross geometry) in classification. Some questions were raised, however, as in the cases of *Dictyonema* v. *Callograptus, Acanthograptus* v. *Thallograptus*, and in the use of simple stipes v. compound stipes. These questions are discussed further below, but the basic classification used here is that of Chapman *et al.* (1996). In our opinion the present level of knowledge of dendroid morphology is inadequate for meaningful cladistic analysis.

Dictyonema J. Hall, 1851 and *Callograptus* J. Hall, 1865

The distinctions between these two genera are not very great. Bulman (1970) considered *Callograptus* to have no dissepiments or to have fewer than *Dictyonema*. Both genera originate in the Middle Cambrian (see Chapman *et al.*, 1996, fig. 2) and range into the Carboniferous. Both genera have rhabdosomes with varying geometry, although each species seems to have a single mode of growth. Both genera have regular branching patterns, and long parallel stipes: and they both exhibit the same range of variations of autothecal and bithecal type. The sole difference seems to be the extent to which dissepiments are developed: *Callograptus* has none or few; *Dictyonema* has common dissepiments. Species of *Callograptus* with no dissepiments are not unlike some of the earliest species of *Dendrograptus* (see Chapman *et al.*, 1996, p. 195) which have fairly ordered branching patterns and long, roughly parallel stipes in bushy, flabellate and possibly conical rhabdosomes. However, in *Dendrograptus* the autothecae remained simple denticulate whereas in *Callograptus* quite varied autothecae were quickly evolved.

The evolutionary scenario deduced by Chapman *et al.* (1996) was of ordered *Dendrograptus* species giving rise in the Middle Cambrian to *Callograptus* and *Dictyonema* by increased development of dissepimental connecting bars between adjacent stipes, with a concomitant restriction in the arrangement of stipes giving rise to flabellate and conical rhabdosomes. In the present work, Fig. 3 extends and revises the relationships deduced in the earlier paper, suggesting that the development of anastomosis and dissepiments were key stages in the evolution of the benthic Dendroidea. This reinforces the earlier suggestion that the method of stipe connection is of more significance taxonomically than is rhabdosome morphology.

Acanthograptus Spencer, 1878 and *Thallograptus* Ruedemann, 1925

The working distinctions between the two genera seem to be that *Acanthograptus* has short twig-like processes developed ventrolaterally from the main stipes, and placed alternatively along the stipe: each twig comprises several thecal tubes, most usually two autothecae (with two bithecae opening near the base of the twig). *Thallograptus*, on the other hand, has stipes and twigs which gradually become thinner as autothecae "peel off" to open as individual tubes projecting either from the sides of the stipe (and, therefore, are superficially twig-like) or projecting ventrally. In both genera the rhabdosomes are usually dendroid and both have compound stipes.

However, the type species *Acanthograptus granti* Spencer, 1878, is less regular than the above generally held concept, although it undoubtedly has twigs amongst a dense branching pattern. Similarly *A. praedeckeri* n.sp. of this paper has a very frequent branching pattern (yet between branches has conspicuous twigs alternating along the stipe) and the stipes are clearly compound. In *A. impar* and *A. murciformis*, both described by Bulman & Rickards (1966), the stipes are compound and a fairly regular sequence of autothecae is maintained. In these species, however, a breakdown of regularity is apparent: not all twigs show the 2+2 pattern, and many autothecae and bithecae open adventitiously, with some autothecae opening erect and isolated—an incipient *Thallograptus* pattern. It would seem that there is a morphological continuum from the simplest of acanthograptids through the most complex, with compound stipes and breakdown of the twig structure, to thallograptids. However, individual evolutionary lineages have not been worked out; although one can conclude that because thallograptids are more common in the Silurian than acanthograptids, (the reverse being true in the Ordovician), then thallograptids probably evolved from acanthograptids. One can predict, therefore, that lineages of increasing stipe complexity may eventually be recognized. For the present most species fall fairly readily into the two genera, but in the present paper *Acanthograptus praedeckeri* n.sp. and *Thallograptus christoffersonae* n.sp. are not easy to distinguish because their rhabdosomes are so similar.

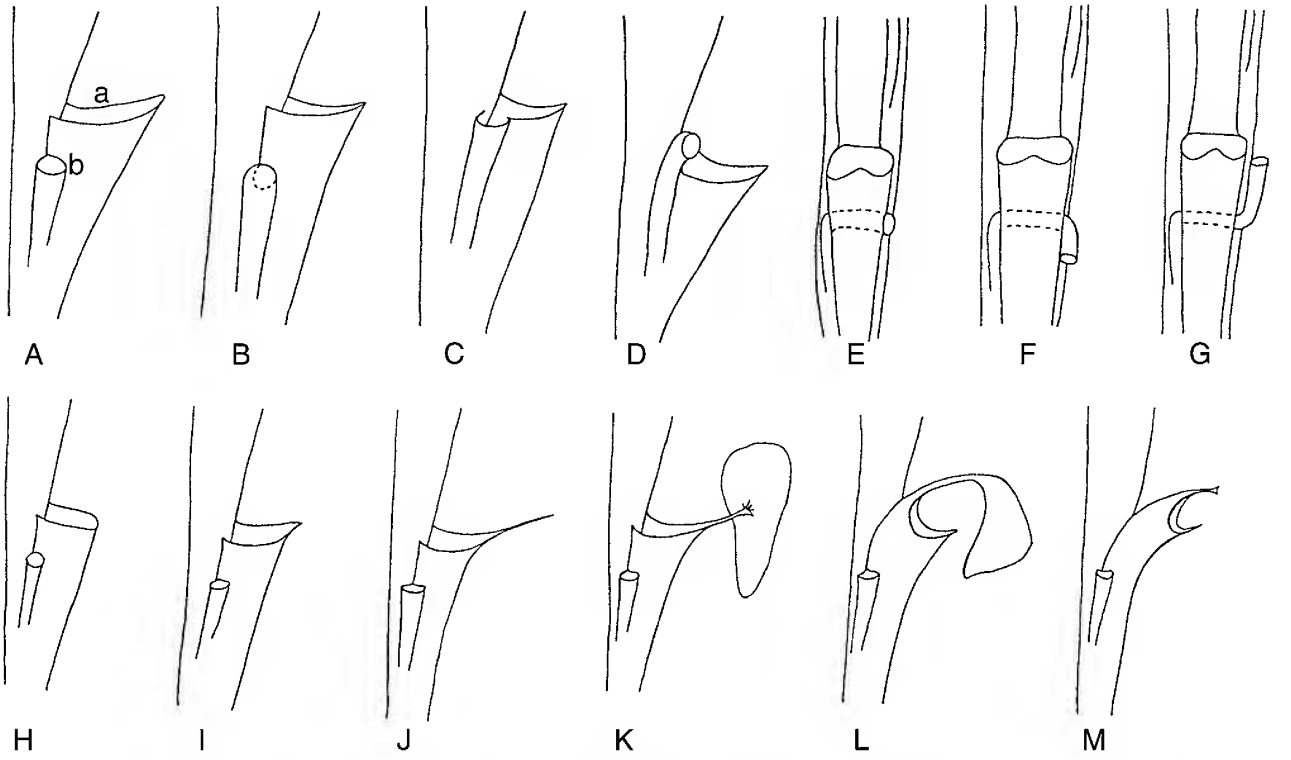

Fig. 4. *A–G*, different types of bithecae: *A*, Bulman's (1928, 1933) Type 1 with bitheca n+1 opening along the lateral wall of autotheca n. This is the most common of autothecal/bithecal relationships; *B,C*, Bulman's (1928, 1933) Type 2 in which the bithecal aperture opens inside the autothecal tube or aperture; *D*, Bulman's (1928, 1933) Type 3 where the n+1 bithecal aperture is located on the dorsal side of the aperture of autotheca n; *E*, Bulman's (1928, 1933) Type 4 in which the bithecal tube n+1 passes between the dorsal wall of autotheca n and the ventral wall of autotheca n+ 1; *F,G*, Bulman's (1928, 1933) Type 5 a modification of Type 4 in which the bithecal tube turns proximally or distally before the bithecal aperture is reached; H–M, autothecal variation in *Dictyonema* species; *H*, autothecal aperture is the termination of a simple tube; *I*, the ventral lip projects as a short, sharp denticle; *J*, the ventral lip projects as a spine which may or may not bifurcate; *K*, the ventral process is adorned with a large shield-like plate; *L*, the dorsal apertural process has plate-like process hanging more or less in front of the aperture; *M*, the apertural region is isolated from the ventral wall of the next autotheca; for the sake of simplicity in *H–M* the Type 1 bithecal arrangement is shown; fuselli omitted; *a*, autothecal aperture; *b*, bithecal aperture; these structures are described or commented upon in various places in the text.

Simple stipes and compound stipes

The question of compound stipes raises problems elsewhere in the dendroid classification. For example Chapman *et al.* (1996) placed *Pseudodictyonema*, with its compound stipes, in a new family, the Pseudodictyonemiidae, which ranges from the Silurian to the Carboniferous. However, some care must be taken: many stipes of species of *Dictyonema* appear superficially to have complex stipe structure because all dendroid thecae are narrow and elongate and in dorsal view a ropy texture may be apparent in well preserved specimens. The complexity has to be such that there is a clear indication of more than one line of stolonal development in any one cross section of the stipe (see, for example, Bulman & Rickards, 1966, figs. 20–23). In this work *Pseudodictyonema graptolithorum* (Počta) is such a case. We suspect that many more species will prove to have compound stipes when suitably preserved material is obtained. Indeed, compound stipes have evolved in a number of lineages, and Chapman *et al.* (1996) recognized four separate origins for this condition.

Dendroid bithecal morphology

Most dendroid species have bithecae comprising small, inconspicuous tubes, with unornamented apertures, which open inconspicuously on the lateral or, occasionally, other parts of the stipe wall. Some open inside the autothecal apertural region. There are, however, more unusual types of bithecae. These were first summarized by Bulman (1927–1967) and he later (1933) gave a more detailed classification of them, defining five types (Fig. 4): Type 1 consisting of the simpler form described above, opening externally just below or level with the autothecal aperture; Type 2 being those forms which open into the autothecal apertural region; Type 3 embracing all forms which open between the apertural region of autotheca *n* and the early free ventral wall of autotheca n+1; Type 4 which grows beyond the point of Type 3 and opens facing laterally; and Type 5 being a morphological step beyond Type 4 in which the bithecal apertural region curves proximally or distally.

The stratigraphy of these morphological types was investigated by Chapman & Rickards (1982) who concluded that the more complex types 4 and 5 (Fig. 4E–G herein) were stratigraphically younger, appearing respectively in the Caradoc and Ashgill series (Ordovician) and being fairly common in Silurian species.

However, even today bithecae are known in relatively few dendroid species and the situation may be more complex than depicted in Fig. 4. For example, Rickards *et al.* (2001) recorded an Iranian late Arenig species of *Dictyonema* in which the bithecae open as long narrow tubes in the spaces of the meshwork, and are isolated for

almost one millimetre of their length. Such a bithecal form does not fall into Bulman's (1933) classification of types, but could be a morphological extension of Types 1, 3, 4 or 5, but presumably not of Type 2.

Based on our present studies *Dictyonema muirae* n.sp. appears also to have aperturally isolated bithecae, but in this case they are conspicuous structures rather overshadowing and overhanging the autothecae (Fig. 13C). Such thecae could develop from the subtype of Type 5 where the bithecal tube curves distally (Fig. 4F,G). Rickards *et al.* (2001) described a comparable structure in their new species, *Callograptus huckriedei*, from the late Arenig of Iran.

These observations suggest that the broad evolution of dendroid bithecae suggested by Chapman & Rickards (1982) is oversimplified: bithecae may become more complicated through time, but Type 5 structures may have been present rather earlier than supposed.

Dendroid autothecal apertural variation

Possibly for reasons of serendipity most of the classic early work on well-preserved (and isolated) dendroids (e.g., Wiman, 1901; Bulman, 1927–1967, 1933; Kozlowski, 1938, 1949) has described species with relatively simple autothecal apertures. Specimens "in the rock" also suggest that most dendroid species have autothecal apertures with a short ventral denticle. Exceptions were described, such as *Dictyonema peltatum* Wiman, 1901 (see Bulman & Rickards, 1966) in which the ventral process develops a large shield-like plate, and in which adjacent plates may coalesce. Other species have the dorsal part of the aperture developed as a spine or process, as in *Dictyonema rhinanthiforme* Bulman, 1933 (see Chapman & Rickards, 1982 for detail). *Dictyonema rhinanthiforme* was originally recorded from the late Arenig or early Llanvirn of Sweden but the Chapman & Rickards (1982) material came from the early Llandovery of the Canadian Arctic region.

In some dendroids, especially *Dictyonema* and *Callograptus*, the autothecal apertures are slightly isolated from the main stipe. These forms may have a ventral denticle, a dorsal process, or both, as in the cases of *D. rhinanthiforme* and *D. elegans* Bulman, 1928 (see also Rickards & Wright, 1997, 1999).

The present collection has a species with isolated autothecal apertures, *D. williamsae* n.sp., although in this case there appear to be no apertural processes. On the other hand *D. warrisi* n.sp. has unusually long ventral apertural spines, a feature we have not seen recorded in dendroids before (except in *Dictyonema* sp. where the spines bifurcate; see Rickards *et al.*, 1995). Further discussion is given under the description of *D. warrisi* n.sp.

In one of the few works on NSW dendroids, Sherrard (1956, table 1) tabulated some characters of NSW Ordovician and Silurian forms assigned to *Dictyonema*, but did not describe any dendroids from the Four Mile Creek area. She described material from Silurian strata at Spring-Quarry Creek, including an indeterminate Llandovery *Dictyonema* sp. and the new (? Ludlow) species *Dictyonema favosum* and *Reticulograptus undulosum*. From the Ludlow of Yass she described ?*Dictyonema* sp. and the new species *Dictyonema vinculosum*, and noted that *D. favosum* was found with the graptolite from Yass that was then called *Monograptus bohemicus* (but see Rickards & Wright, 1999).

Systematic palaeontology

Material studied here has been collected by GHP over many years, by Dr Chris Jenkins and by RBR, AJW and GHP in 2000, with assistance from Dr Ian Percival and Ms Lucy Muir in 2000. Material described herein is deposited in the Australian Museum, Sydney and bears the prefix AM F. Localities prefixed by the letter W refer to collections made in November, 2000; those with the prefix F refer to collections made by Packham, and those with the prefix BF refer to collections made by Jenkins (1973). Although some of these localities are probably the same (e.g., W885, BF14 and F14) we have referred to them with their original prefixes or locality number in each case.

Class Graptolithina Bronn, 1849
Order Dendroidea Nicholson, 1872
Family Dendrograptidae Roemer, *in* Frech, 1897
Dendrograptus J. Hall, 1858

Type Species. *Graptolithus hallianus* Prout, 1851; subsequently designated by J. Hall (1862).

Dendrograptus avonleaensis n.sp.

Figs. 5A, 6A,B

Material. HOLOTYPE AM F114646a-b and PARATYPES AM F114650 and AM F114766, all from F14, Bridge Creek.

Etymology. After the property "Avon Lea" on which F14 is located.

Diagnosis. *Dendrograptus* with robust funnel-shaped rhabdosome at least 15 mm long and 18 mm at its widest; branching in broad zones; stipes with a dorsoventral width of 0.50–0.60 mm and a lateral width of 0.20–0.40 mm; autothecal spacing 18–20 in 10 mm.

Description. The holotype (Fig. 6B) displays a distal array of at least 48 stipes arranged in a broadly conical fashion with two major branching zones. These distal stipes diverge some 3.5 mm above the visible base of the specimen, but they do not arise from a solid stem: tightly clustered stipes are visible in the densely packed area. The overall shape is, therefore, funnel-shaped with a proximal constriction. In one or two places the stipes are visible in profile when the autothecae, spaced at 18–20 in 10 mm, can be seen to be of simple denticulate type (Fig. 4I). The lateral stipe width is 0.40 mm proximally, falling to 0.20 mm most distally, suggesting some cortical thickening as the colony ages. Two other specimens (e.g., Fig. 5A) are fragments from beyond the zone of expansion. They show some of the above-described features but less well-displayed.

Remarks. As described by Chapman *et al.* (1996) some *Dendrograptus* species can be quite well ordered; this is one such species, having a broadly conical, funnel-shaped form and rough branching zones. *Dendrograptus avonleaensis* n.sp. has a superficial resemblance to *Calyptograptus cyathiformis* Spencer, 1878 from the Niagara Limestone, but that species has more frequent and irregular branching and a robust stem; the thecae of *C. cyathiformis* are not known. *Dendrograptus avonleaensis* differs from *D. ashburniaensis* n.sp. herein in that the latter has a thecal

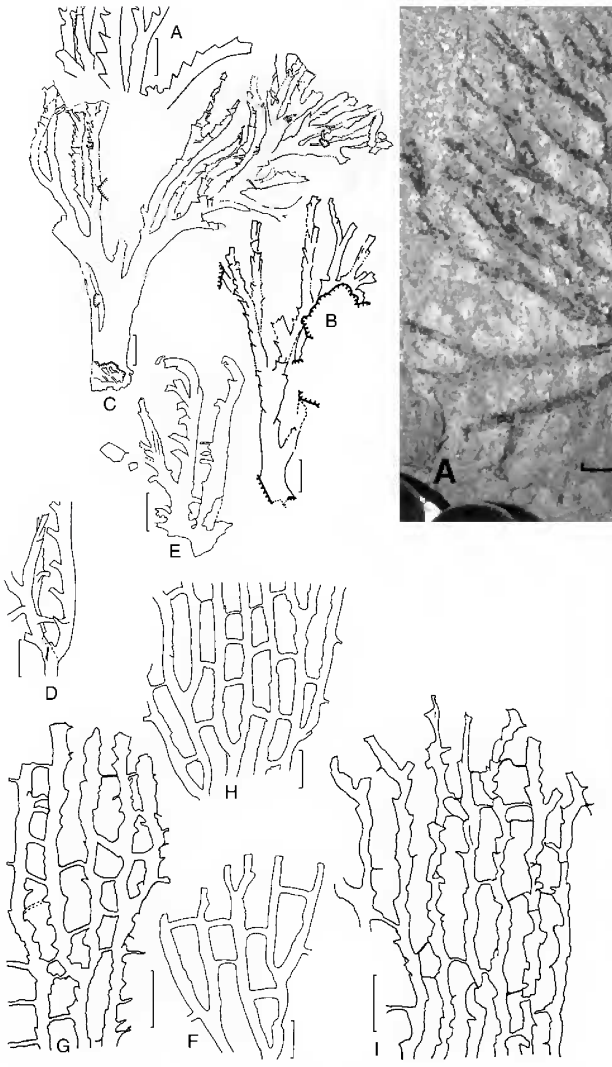

Fig. 5. *A*, *Dendrograptus avonleaensis* n.sp., holotype AM F114646b, BF14; *B,C*, *Dendrograptus ashburniaensis* n.sp., respectively AMF114566 and holotype 114567, both from F14; *D–F*, *Dictyonema williamsae* n.sp., respectively holotype AM F114565, AM F114758, part of basal holdfast present, and holotype AM F114565, showing dorsoventral view of stipes, all from W885; *G*, *Dictyonema* cf. *delicatulum*, AM F114648a, W885; *H*, *Dictyonema venustum*, AM F114048a, W885; *I*, *Dictyonema falciferum*, AM F114750, F14. Scale bars 1 mm; in *B* and *C*, hatched areas indicate that specimen is obscured by sediment.

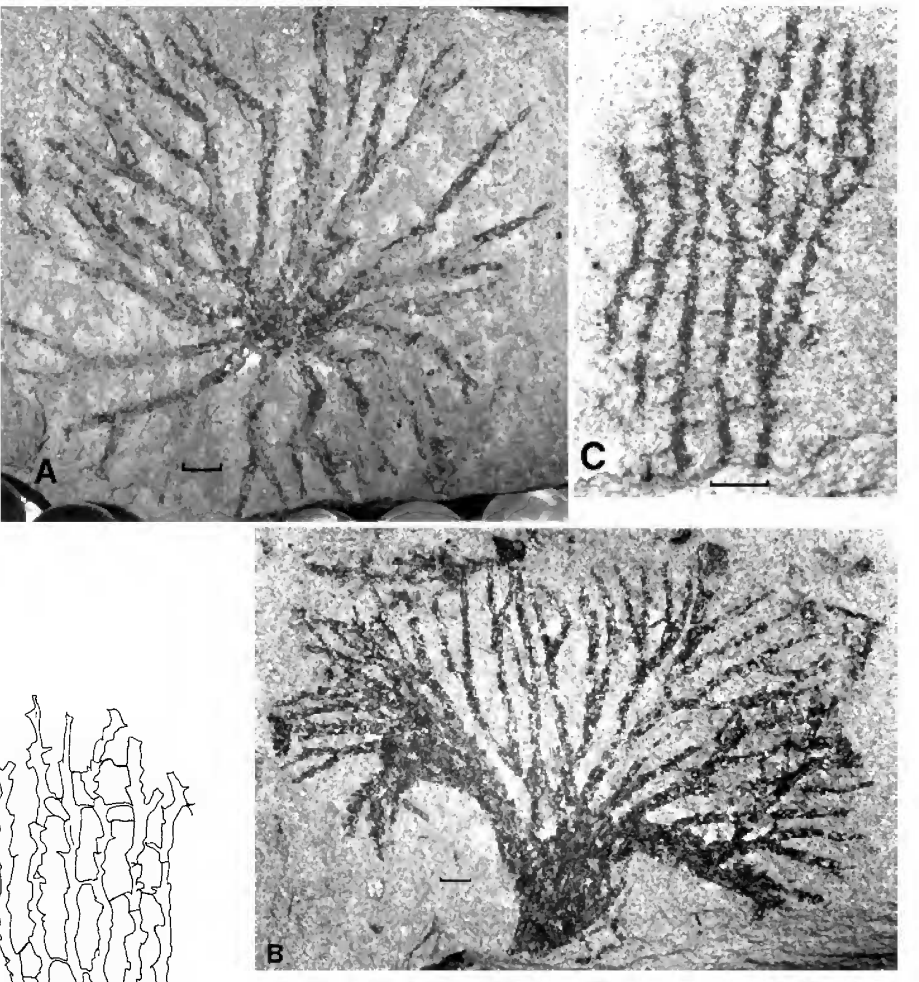

Fig. 6. *A,B*, *Dendrograptus avonleaensis* n.sp., respectively AM F114650 and holotype AM F114646a, both from BF14; *C*, *Dictyonema* cf. *delicatulum*, AM F114749, F14. Scale bars 1 mm.

spacing of 36 in 10 mm, almost twice that of the former; and *D. ashburniaensis* develops a thickened stem proximally.

Dendrograptus ashburniaensis n.sp.

Fig. 5B,C

Material. HOLOTYPE AM F114567 and PARATYPE AM F114566, both from F14, Bridge Creek.

Etymology. After the nearby property of "Ashburnia", at the former Four Mile Creek post office.

Diagnosis. *Dendrograptus* with an unusually high thecal spacing of 36 in 10 mm, and irregular and frequent branching from a robust stem region.

Description. The overall colony shape may be irregularly dendroid, developed from a robust stem about 1 mm thick. Branching is frequent and irregular, at least once each 1–2 mm of stipe. The lateral stipe width decreases immediately away from the stem or main branches to approximately 0.30 mm; the dorsoventral width is about the same. Autothecae are visible where branches have been turned into the profile position, and seem to be of simple denticulate type, numbering 36 in 10 mm on both the specimens available. No trace of bithecae has been found. The specimen illustrated in Fig. 5B may have a relatively narrow holdfast at its base. The holotype has at least 21 terminal stipes after only 13 mm of growth, but the number at this stage could be much greater as several branches are broken.

Remarks. Most *Dendrograptus* species have thecae relatively widely spaced in the range of 12–20 in 10 mm, so *D. ashburniaensis* is unusual in this respect with its thecal spacing of 36 per 10 mm. *Dendrograptus* species are uncommon in the Silurian and we can equate our Bridge Creek specimens with none of them. *Dendrograptus parallelus* Shrock, 1928 from the Silurian of Indiana has a similar rhabdosome but the branching is much more widely spaced. *Dendrograptus phainotheca* Gurley, 1896 also has very widely spaced branching and an autothecal spacing of only 18 in 10 mm. Described Ordovician species have wider thecal spacings than *D. ashburniaensis* and mostly

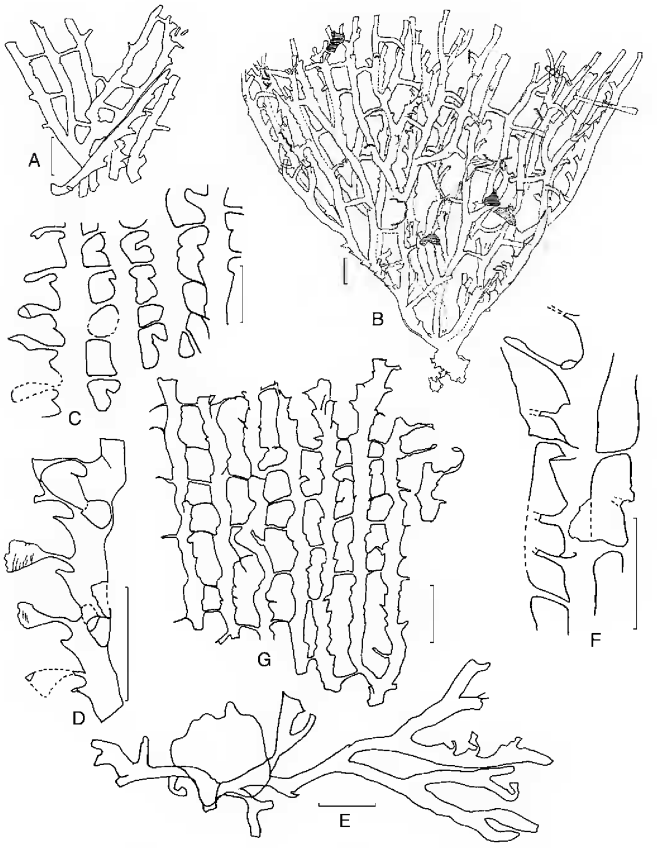

Fig. 7. *A*, *Dictyonema venustum*, AM F114751, BF28; *B*, *Dictyonema williamsae* n.sp., holotype AM F114565, W885; *C–E*, *Dictyonema jenkinsi* n.sp., respectively AM F114747, F14, holotype AM F114716, BF24; and AM F114761, F14, holdfast region attached to roughly circular object, possibly a pebble; *F,G*, *Dictyonema paululum australis* n.subsp., AM F114757, parts of holotype, BF14. Scale bars 1 mm; on B hatching indicates specimen obscured by sediment, stipple indicates badly preserved area, and horizontal shading indicates fractures in rock.

narrow stipes with more widely spaced branches. *Dendrograptus avonleaensis* n.sp. is the nearest form in general appearance but differs in having a much wider thecal spacing (see previous description).

The species described as *Dendrograptus* sp. B. by Rickards *et al.* (1995) has more widely spaced branching points than *D. ashburniaensis*, and *D.* sp. B. may be roughly compared with *D. parallelus*. Of the other Australian *Dendrograptus* species, *D.* sp. of Rickards & Wright (1997) from the *inexpectatus* or *kozlowskii* Biozone (Ludlow, Silurian) has a similar branching frequency but a much wider thecal spacing (15–20 in 10 mm). *Dendrograptus ashburniaensis* and *D. avonleaensis* are the best-preserved Australian *Dendrograptus* species so far described.

Dictyonema J. Hall, 1851

Type species. *Gorgonia retiformis* J. Hall, 1843; subsequently designated by Miller (1889).

Remarks. As there is often considerable difficulty, in the absence of holdfasts or siculate origins, in assigning a benthic or planktic mode to dendroid graptolite specimens, here we follow the traditional, conservative approach, as did Rickards *et al.* (1994), in using *Dictyonema* in its traditional sense to include planktic forms.

Dictyonema cf. *delicatulum* Lapworth, 1881

Figs. 5G, 6C

cf. 1881. *Dictyonema delicatulum* Lapworth; Lapworth, p. 172, pl. 7, fig. 2a,b.

cf. 1928. *Dictyonema delicatulum*, Lapworth, emend.; Bulman, p. 51–52, pl. 6, figs. 7–11.

Material. AM F114648a, AM F114749 and AM F114769–71, all from F14, Bridge Creek.

Description. The best-preserved rectangular fragment of rhabdosome embraces eight stipes with several branching points, and measures 4×8 mm. Stipe spacing is about 20 in 10 mm, dissepiments (which are conspicuous) 14–18 in 10 mm, and the autothecal spacing 20–25 in 10 mm. Dissepiments vary from quite thread-like to a width of 0.10 mm, and are mostly disposed at right angle to the stipes. The lateral stipe width is 0.20–0.30 mm, but the dorsoventral stipe width cannot be measured in the absence of profile stipe views. There is, however, a suggestion of the autothecae, enabling a rough measurement, but the exact nature of the autothecal apertures cannot be ascertained, although one specimen (AM F114769) does show thecae with a long ventral denticle or spine.

Remarks. The material closely matches Bulman's (1928) redescription of the species, differing only in the dissepimental spacing (14–18 in 10 mm in the Australian specimens, compared with 10–12 in 10 mm in European specimens). We are, however, unsure of the exact nature of the autothecal apparatuses in our material, having established only that they are denticulate.

Dictyonema williamsae n.sp.

Figs. 5D–F, 7B, 8A

Material. HOLOTYPE AM F114565 and three PARATYPES AM F114652a-b, AM F114758 and AM F114772a-b, all from F14, Bridge Creek.

Derivation of name. After Norma Williams of "Ashburnia".

Diagnosis. Robust, conical *Dictyonema* rhabdosome, developed from a holdfast, each of four primary stipes with different branching patterns; stipes are connected by robust dissepiments, each of which is slightly arched distally; autothecae are aperturally isolated tubes without marked denticulation; autothecal spacing 13 in 10 mm; dissepimental spacing 6–7 in 10 mm; stipe spacing 8–12 in 10 mm; lateral stipe width maximum 0.30 mm; dorsoventral stipe width 0.60–0.70 mm.

Description. The rhabdosome is conical, some 14 mm high by 14 mm wide at the aperture of the cone. It derives from a small basal disc or holdfast. The most striking feature of the colony is the rectangular interstipe spaces defined by robust dissepiments and stipes of not much greater width; dissepiments are 0.15–0.20 mm wide and stipes in lateral view 0.15–0.30 mm. Of the several main stipes, which arise from the holdfast region, two produce at least 27 of the 34 peripheral stipes, so that one could say that at least three quarters of the cone is built by branchings from only two stipes. There are no obvious branching zones.

When seen in full profile the autothecae are aperturally isolated but without marked denticulation (Fig. 5D,E). In places they are difficult to distinguish from partially

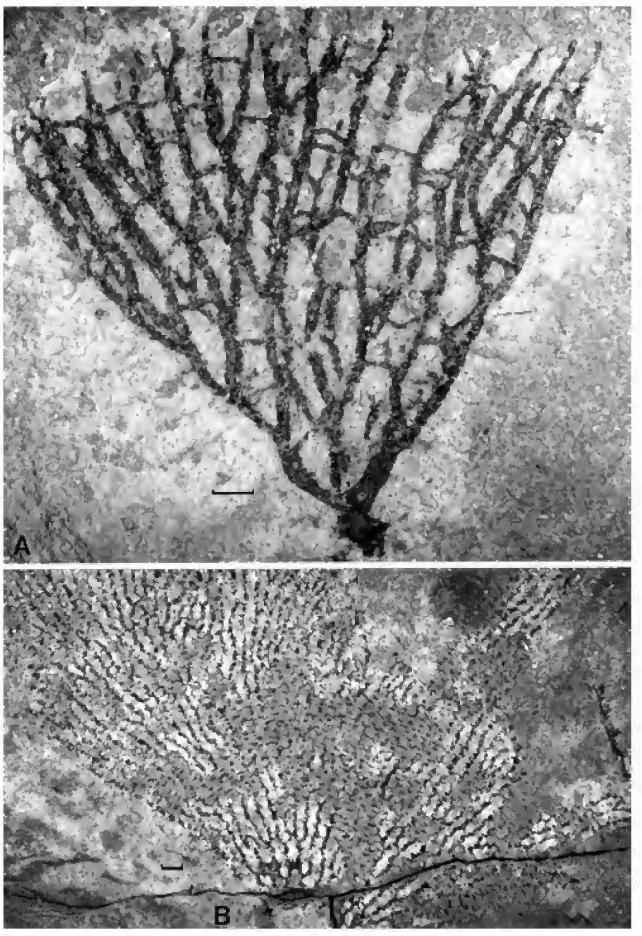

Fig. 8. *A*, *Dictyonema williamsae* n.sp., holotype AM F114565, F14; *B*, *Dictyonema falciferum*, AM F114750, F14. Scale bars 1 mm.

preserved dissepiments which have a similar width; it is possible, though unproven, that the dissepiments are actually autothecal transfers from one stipe to the adjacent stipe.

Remarks. *Dictyonema williamsae* is an unusual form having a low thecal spacing which eliminates comparison with most other dictyonemids. *Dictyonema inequabile* Bulman from the late Llandovery of Scotland has a similar arrangement of stipes and rhabdosome, but differs in having a less regular meshwork and very variable lateral stipe widths and equally variable dissepimental widths. The autothecal type and spacing is unknown in *D. inequabile*. However, *D. inequabile* is undoubtedly the closest form to *D. williamsae*, most dictyonemids having a much higher thecal spacing. *Dictyonema obpyriforme* (Gurley in Bassler, 1909) has a similar stipe arrangement but all measurements differ markedly. Many of the Silurian dictyonemids described by Bassler (1909) and Ruedemann (1947) have stipes that are much too robust for comparison with *D. williamsae* even when the stipes have rectangular interstipe spaces. Of the species described by Bouček (1957) *Dictyonema elongatum* is closest to *D. williamsae* in rhabdosomal and stipe dimensions, but its thecae appear to be simpler, its stipe spacing narrower (14–16 in 10 mm) and it dissepimental spacing wider (2–6 in 10 mm).

Dictyonema falciferum Bulman, 1928

Figs. 5I, 8B, 9C, 10A

1928. *Dictyonema falciferum*, n.sp.; Bulman, p. 53–56, pl. 5, figs. 1–3, text-figs. 27–29.

Material. AM F114750 from F14, Bridge Creek.

Description. The flabellate appearance of this large, well-preserved colony, some 27 mm by 40 mm, may be a preservational feature: there is a slight suggestion that it represents one half of a conical colony. The counterpart is, unfortunately, not available. There are at least 94 peripheral stipes developed, spaced at 16 in 10 mm, each with a lateral width of 0.20–0.25 mm. Branching zones are about every 1 mm proximally and 2–3 mm towards the periphery of the colony, complicated somewhat by local anastomosis. Dissepiments are spaced at 6–8 in 10 mm, possibly a little closer in places. Autothecae are denticulate but not otherwise ornamented. Bithecae are not developed with certainty, possibly rather bulbous aperturally, reflected in the slightly sinusoidal growth of the stipes when viewed dorsoventrally; the last feature is more conspicuous toward the periphery of the colony.

Remarks. This specimen differs only slightly from Bulman's type specimens, the stipes in the Bridge Creek specimens being a little more slender on average and the thecal spacing slightly wider (15? in 10 mm compared with 16–20 in 10 mm). In most aspects our form is very close indeed to the types, which were described from the upper Llandovery (approximately *crispus* Biozone) of Shropshire, Wales and Scotland (Bulman, 1928: 50). This is the first record of this species from Australia.

Dictyonema venustum Lapworth, 1881

Figs. 7A, 9D, 10B–D

1881 *Dictyonema venustum* Lapworth; Lapworth, p. 171–172, pl. 7, fig. 1a–c.
1928 *Dictyonema venustum*, Lapworth, emend.; Bulman, p. 61–63, pl. 5, figs. 6–8, text-fig. 34.

Material. AM F114648a-b, AM F114649, AM F114717a-b and AM F114873, all from F14; AM F114751 from BF 28, all Bridge Creek.

Diagnosis. Large *Dictyonema* characterized by a striking rectangular meshwork of stipes and fairly robust dissepiments; at least 30 mm long, possibly conical, with irregular stipe branching; stipes 10–18 in 10 mm; denticulate autothecae spaced at 20–30 in 10 mm; dissepimental spacing 5–8 in 10 mm.

Description. Our largest specimen is a fragment of a large rhabdosome but it is not possible to say whether or not it is conical. A striking rectangular meshwork of stipes and fairly robust dissepiments typifies the colony. Stipes have a lateral width of 0.20–0.35 mm and a dorsoventral width of about 0.40 mm, whereas the dissepimental width is 0.10–0.25 mm. Stipe spacing ranges from 10–18 in 10 mm, the mean being 14–15 and the lower values nearer the proximal end. Stipe branching seems quite irregular. There is a limited amount of anastomosis in the stipe pattern. No bithecae have been detected.

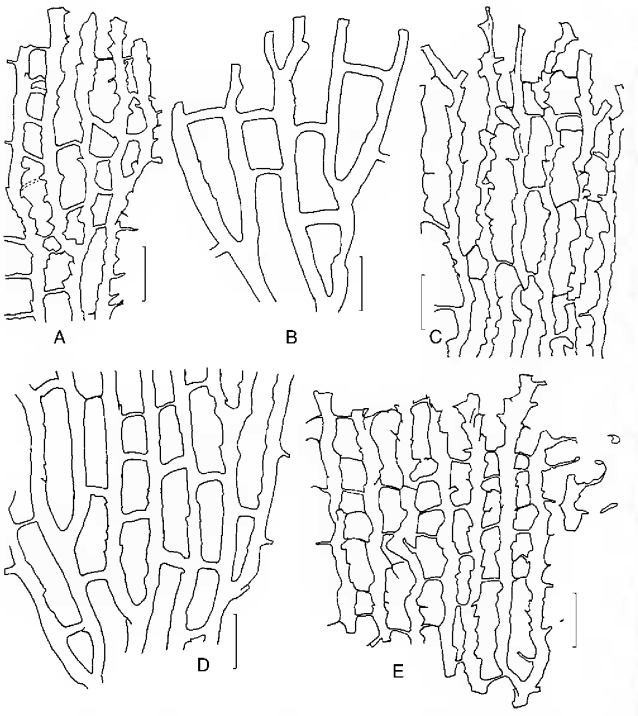

Fig. 9. *A–E*, illustrating contrasting stipe and dissepimental patterns in distal parts of colonies: *A*, *Dictyonema* cf. *delicatulum*, AM F114749; *B*, *Dictyonema williamsae* n.sp., AM F114565, holotype; *C*, *Dictyonema falciferum*, AM F114750; *D*, *Dictyonema venustum*, AM F114648a, F14; *E*, *Dictyonema paulului australis* n.subsp., holotype AM F114757. Scale bars 1 mm.

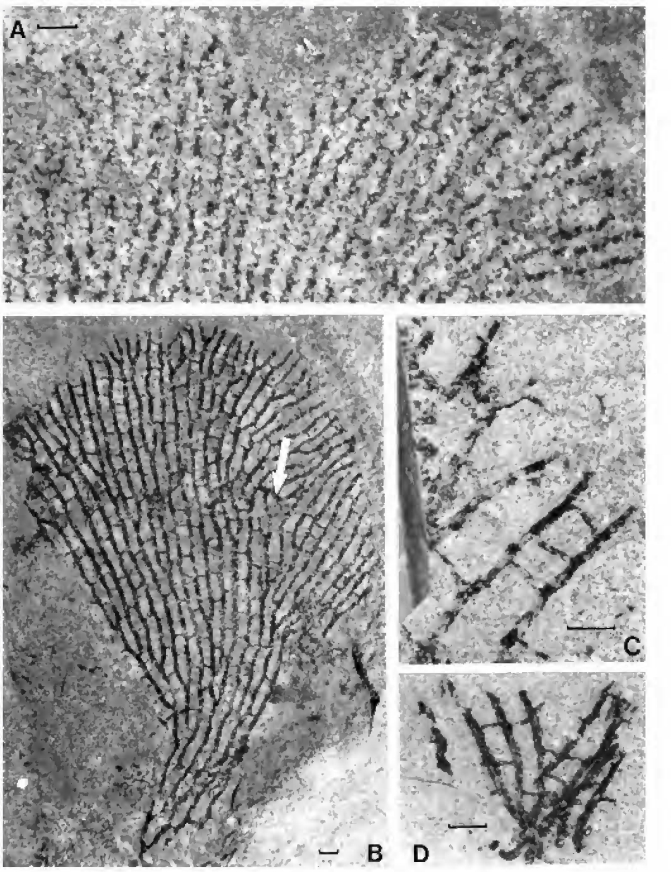

Fig. 10. *A*, *Dictyonema falciferum*, AM F114750, F14; *B–D*, *Dictyonema venustum*, respectively AM F114648 and AM F114873, both BF14, and AM F114751, BF28. Scale bars 1 mm; arrow on *B* indicates damaged area discussed in text.

Remarks. In most respects our material is close to Bulman's (1928) redescription of the type and other material, differing only in having a slightly closer thecal spacing (20 in 10 mm compared with 16–17 in 10 mm) and slightly more slender dissepiments. The irregular branching mode is very similar to that on the Welsh and Scottish material described by Bulman (1928: p. 643), as is the stipe spacing, stipe widths and dissepimental spacing.

The largest specimen exhibits a damaged and repaired area (Fig. 10B, arrowed). In this region are two short, incomplete stipes whereas one very robust stipe tracks left to right, crosses one stipe and then anastomoses with the next one, which then terminates. The stipe crossed over by the robust, laterally-directed stipe continues to grow and fills the gap caused by the damage, so that by the rhabdosomal periphery a normal stipe arrangement is restored. The most likely explanation of the damage is that a hole was punched into the stipe array, separating the stipes and breaking off some of them.

Dictyonema paulului australis n.subsp.

Figs. 7F,G, 9E, 12A

Material. HOLOTYPE AM F114757a-b and PARATYPES AM F114758 and AM F114773–4, all from BF14, Bridge Creek.

Derivation of name. Suggesting that it is a geographical subspecies.

Diagnosis. Conical *Dictyonema paulului* with 16 stipes in 10 mm; autothecae denticulate and spaced at 20 in 10 mm; dissepiments spaced at 12–20 in 10 mm; stipe lateral width 0.20 mm and dorsoventral width 0.50 mm.

Description. The largest specimen is about 30 mm long and all the rhabdosomal fragments are characterized by slender stipes with a marked parallel arrangement connected by very slender dissepiments of 0.05 mm. Branching is very approximately zoned, every 1.5–2.5 mm, being more widely spaced distally. Dissepimental spacing is closest distally, at 20 in 10 mm, about one per autotheca, but proximally may rise to 12–13 in 10 mm. The autothecae are certainly denticulate, even spinose in profile, and the termination may possibly be spatulate rather than pointed. It is difficult to distinguish autothecal processes from dissepiments in this material. The overall appearance of the stipes is gently undulating with a serrated margin in places (Fig. 7G).

Remarks. *Dictyonema paulului australis* occurs at the same late Llandovery level as the nominate subspecies and, although very elegant and slender, is fractionally more robust than that form, with a more varied dissepimental spacing. In the nominate subspecies, the stipe spacing is slightly wider (16 in 10 mm compared with 20 in 10 mm) and the rectangular interspaces are narrower and often longer. The differences seem consistent in all material, and we regard *D. p. australis* as a geographical subspecies of *D. paulului* Bulman, 1928.

Dictyonema jenkinsi n.sp.

Figs. 7C–E, 11A,B

Material. HOLOTYPE AM F114716 and PARATYPES AM F11461, AM F114747–8 and AM F114776–8, all from F14, Bridge Creek.

Derivation of name. In honour of Dr Chris Jenkins who collected many of the graptolites in our collections.

Diagnosis. Large, ?conical *Dictyonema* rhabdosome developed from basal holdfast; thecae with unique, plate-like outgrowths of dorsal, apertural processes; autothecal apertures slightly isolated; bithecae bulbous aperturally.

Description. One rhabdosomal fragment (Fig. 7E) is of a holdfast with three or four main stipes developed from it; stipe division is close to the holdfast and, although this specimen is preserved in "plan" view, it suggests that a conical rhabdosome develops from the holdfast. Another large fragment of rhabdosome, of which Fig. 7C is a part, indicates an overall large colony perhaps 25 mm long. Stipes are spaced at 14 in 10 mm, have a lateral width of about 0.50 mm, and are connected by hair-like dissepiments spaced at 18–20 in 10 mm and by occasional anastomosis. The stipe spacing is, therefore, slightly closer than the autothecal spacing, which is 16 in 10 mm. The autothecae have slightly isolated thecal apertures, a denticulate ventral apertural process (Fig. 7D) and a conspicuous dorsal apertural process, composed of fuselli, which grows to a plate-like form expanding away from the apertural region.

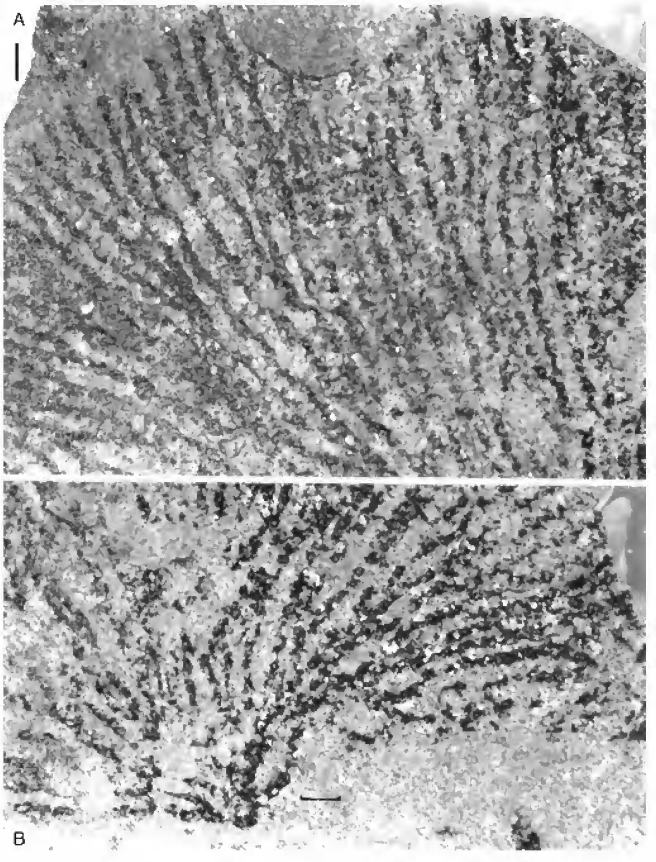

Fig. 11. *A,B*, *Dictyonema jenkinsi* n.sp., AM F114748, respectively distal thecae and proximal end close to holdfast, F14. Scale bars 1 mm.

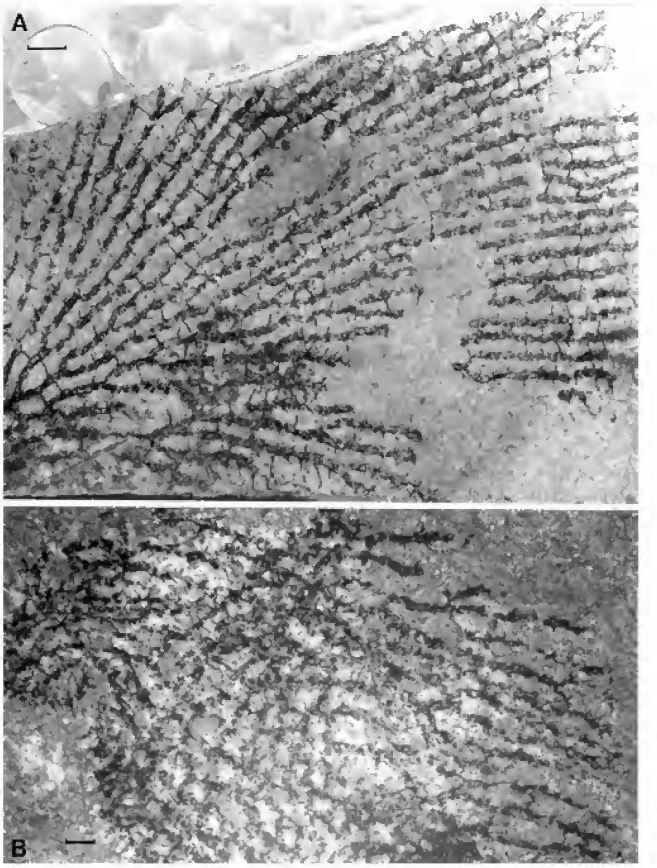

Fig. 12. *A*, *Dictyonema paululum australis* n.subsp., AM F114757, holotype, BF14; *B*, *Dictyonema warrisi* n.sp., holotype AM F114647a, F14. Scale bars 1 mm.

Sometimes it hangs downward slightly, presumably overhanging the apertural region. The dorsoventral width is 0.80 mm, excluding the large process, but up to 1.30 mm including it. Bithecae can be detected on the holotype as bulbous growths positioned dorsally of the autothecal apertural region; they alternate along the stipe (Fig. 7D).

Remarks. The autothecal processes make *D. jenkinsi* a unique species. Similar plate-like growths are developed on *D. peltatum* Wiman, 1901, but these are modified ventral apertural processes. The hydrodynamic function may be similar, of course, as suggested by preliminary work by one of us (R.B.R.). The bithecae may be of Bulman's (1928) type 5; that is, not dissimilar to the bithecae in *D. cavernosum* Wiman, 1901 (see Bulman & Rickards, 1966).

Dictyonema muirae n.sp.

Fig. 13A–D

Material. HOLOTYPE AM F114762 and PARATYPES AM F114763–4 and AM F114775, all from F14, Bridge Creek. PARATYPE AM F14779 from BF24, Wallace Creek.

Derivation of name. After Lucy Muir, in recognition of her skilled graptolite collecting.

Diagnosis. *Dictyonema* with unusually close thecal spacing of 40 in 10 mm, of denticulate autothecae, and with very unusual isolated, curved bithecae; sparse dissepiments.

Description. The rhabdosome grows from a holdfast with rapid and irregular branching taking plate (Fig. 13D). Irregular branching is maintained in the specimens we have, and perhaps because of the frequency of branching, dissepiments are difficult to identify and possibly few in number. Stipe spacing is 14–20 in 10 mm depending upon how divergent the growth is at any point. The dorsoventral stipe width is about 0.60 mm, and the lateral stipe width 0.30–0.40 mm. The autothecae are markedly denticulate (Fig. 13B) and are spaced at 40 in 10 mm. Associated with the autothecae (Fig. 13C) are curved, narrower tubes, the apertures of which face distally. These are probably bithecae and they may be a modified form of Bulman's (1928) Type 5 where the bithecal apertural region extends in an isolated manner. The overall colony form is not known.

Remarks. The combination of very close autothecal spacing with unusual bithecae makes *D. muirae* a unique, unusual species of *Dictyonema*. The irregular, frequent, and divergent branching, coupled with the presence of dissepiments, supports attribution to *Dictyonema* rather than *Callograptus*. The individual stipes look not unlike robust *Dendrograptus* species.

Dictyonema warrisi n.sp.

Figs. 12B, 13E–G

Material. HOLOTYPE AM F114647a-b and PARATYPES AM F114629b and AM F114717, all from F14, Bridge Creek.

Derivation of name. After Dr Bevan Warris who first mapped the Angullong Syncline in detail.

Diagnosis. Unusual *Dictyonema*, ?conical, 3 cm long, with pronouncedly spinose autothecae, closely spaced at 28 in 10 mm; lateral stipe width 0.20–0.30 mm; dorsoventral stipe width 0.20–0.35 excluding spines which may be 1 mm long.

Description. The largest rhabdosome, possibly conical, is 30 mm long and 14 mm wide. A second, smaller (15 mm by 7 mm) specimen, possibly part of the same conical rhabdosome, crosses the first. The overlap area of the two creates an initially misleading *Desmograptus* appearance. On this large specimen the spinose thecae are difficult to see but are present. Dissepiments vary from fine and hair-like to more robust and irregular (Fig. 13E). Dissepimental spacing is about 12 in 10 mm but rather variable from place to place. The isolated stipe fragment (Fig. 13F) is in full profile and shows the ventral apertural spines well though not to full length. The bithecal apertures open in the angle between the autothecal aperture and the ventral wall of the next autotheca (thecae 1, 3, and 5 on Fig. 13F). They are of Bulman's (1928) type 4.

Remarks. Very few *Dictyonema* species are known with long autothecal spines. Rickards *et al.* (1995, p. 22, fig. 14G) illustrated *Dictyonema* sp. E with long, bifurcating ventral spines (see description of *Dictyonema* sp. 1 below). *Dictyonema warrisi* is distinct from that form in that the spines do not bifurcate.

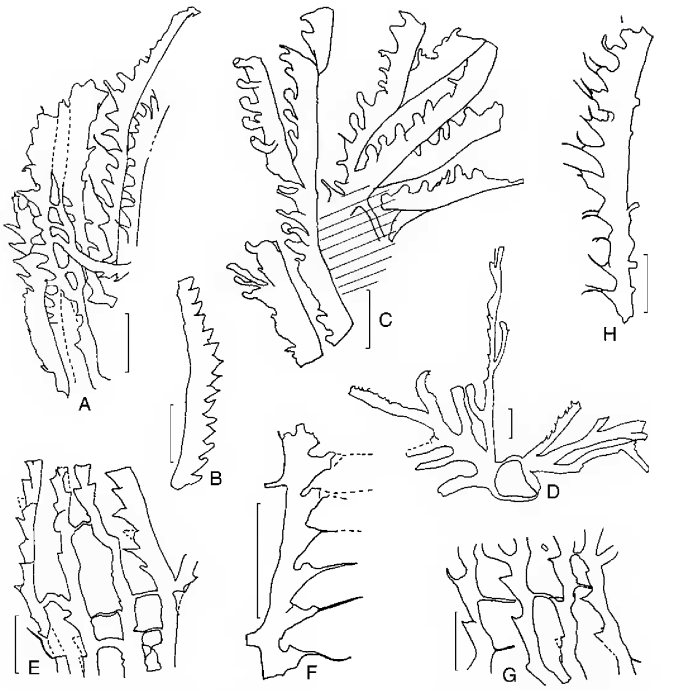

Fig. 13. *A–D, Dictyonema muirae* n.sp., respectively AM F114763, BF14, AM F114775, F14, holotype AM F114762, F14, and AM F114764, BF14 proximal part of colony attached to pebble of phosphate; *E–G, Dictyonema warrisi* n.sp., respectively AM F114647, F14, holotype AM F114717, W885 and AM F114647, F14, with stipes more proximal than E; *H, Dictyonema* sp. 1, AM F11475, F14. Scale bars 1 mm; shading on *C* indicates badly preserved area.

Dictyonema sp. 1

Fig. 13H

Material. AM F114754 from F14, Bridge Creek.

Description. One small stipe fragment shows 10–11 thecae spaced at 20 in 10 mm, each provided with two spines. It is not certain, but it seems likely, that these spines grow from the ventral region of the autothecal aperture. No traces of bithecae are visible. The dorsal wall shows the bases of 3–4 dissepiments giving a dissepimental spacing of about 8 in 10 mm. The dorsoventral width excluding processes is up to 0.75 mm, and up to 1.25 mm including spines. It is uncertain whether the spines are formed from bifurcation of one ventral denticle, or whether two spines arise independently from the ventral apertural wall.

Remarks. *Dictyonema* sp. 1 differs from *D. warrisi* in having a wider thecal spacing (20 compared with 28 in 10 mm) and in having two thecal spines. *Dictyonema* sp. E of Rickards *et al.* (1995: 22, fig. 14G) has a bifurcating ventral process and a thecal spacing of 30 in 10 mm. This latter form is from the *nilssoni* Biozone (Ludlow) and the thecal spines are more like those of *D. cervicorne* Holm, 1890, from the Ordovician of Scandinavia (although lacking the bulbous bithecae of that form) than those of *D. warrisi*.

Callograptus J. Hall, 1865

Type species. *Callograptus elegans* J. Hall, 1865.

Callograptus bridgecreekensis n.sp.

Figs. 14A, 15A,B

Material. HOLOTYPE AM F114569a-b from F14, Bridge Creek.

Derivation of name. After the stream at the type locality.

Diagnosis. *Callograptus* with a robust stem, consisting of numerous tubes, 10 mm long and 1.2 mm wide; no dissepiments; spacing of sharply denticulate autothecae 30–35 in 10 mm, bithecae small, inconspicuous tubes.

Description. A single, large rhabdosome 35 mm long by 27 mm wide is developed from a robust stem region, itself about 10 mm long and 1.2 mm at its widest. The stem may originate from a small holdfast about 2 mm wide. The stem comprises a considerable bundle of tubes, some ending as thecal apertures along its length (Fig. 15B). The rhabdosome has over 50 terminal stipes preserved. The stipes are parallel and divergence at branching points is at a low angle: stipe frequency is 19–21 in 10 mm. Branching is frequent and irregular but a relatively small number of "main stipes" seem to give rise to the many terminal stipes. There are four, possibly five "main stipes" on the specimen: one (possibly two) arises quickly at the top of the stem region; the other three develop within 5 mm of the top of the stem. This arrangement of fan-like fronds, coupled with the presence of a robust stem, suggests an overall fan-shaped rather than conical colony. There are no dissepiments. Lateral stipe width proximally is 0.40–0.60 mm and most distally 0.20–0.30 mm. The dorsoventral stipe width is 0.40–0.50 mm. Autothecal spacing is 30–35 in 10 mm. The autothecae are sharply denticulate, possibly slightly spatulate, but not spinose. Bithecae are small, inconspicuous tubes opening in the axil between autothecal aperture and the free ventral wall of the next autotheca.

Remarks. The arrangement of fan-like branches is not uncommon in *Callograptus* (e.g., the type species *C. elegans*), and recalls to some extent *Licnograptus* Ruedemann, 1947 (wherein thecal details are unknown). Callograptus, like *Dendrograptus*, is uncommon in the Silurian. *Callograptus bridgecreekensis* differs from the two Silurian forms briefly discussed by Bulman (1928), and from the three species described by Bouček (1957): *C. conjunctus* Bouček exhibits stipe anastomosis and the stipes are more robust and widely spaced; *C. flabellatus* Bouček (? = *Dictyonema*) has numerous dissepiments; and *C. scopatus* Počta is a markedly more robust species with very widely spaced stipes. Of the North American forms described by Bassler (1909), *C. minutus* Spencer, 1878, *C. multicaulis* Spencer, 1878 and *C. niagarensis* Spencer, 1878 (see description below) have small, bushy rhabdosomes, and *C. strictus* Gurley, 1896 (*? = Dictyonema*) has numerous dissepiments. Ruedemann (1947) considered an additional species, *C. pulchellus* Shrock, 1928 (see also Rickards & Wright, 1997), which has dissepiments but similar dimensions. The form described as *Callograptus ?pulchellus* Shrock subsp. 1 by Rickards & Wright (1997, fig. 4D) has more undulating, divergent stipes than *C. bridgecreekensis*, whereas *C. ?pulchellus* Shrock subsp. 2 of Rickards & Wright (1997) is insufficiently known but is possibly referable to *C. bridgecreekensis* (although subsp. 2 is from the late Ludlow).

Callograptus rigbyae n.sp.

Fig. 14B,C

Material. HOLOTYPE AM F114651a-b, from BF28 from an unnamed tributary W of Bridge Creek; and PARATYPE AM F114643 from W885, Bridge Creek.

Derivation of name. After Dr S. Rigby, well-known graptolite worker.

Diagnosis. Small, robust *Callograptus* with small holdfast or short stem; usually preserved in "plan" view, branching in well-marked zones, six of which give a 10 mm colony spread; dissepiments absent; autothecae 20 in 10 mm approximately.

Description. The rhabdosomes are spread in a "plan" view but are sufficiently well-preserved to conclude that dissepiments are absent. Stipes have a lateral width of 0.20–0.30 mm and there are five branching zones in a distance of 5 mm from the origin resulting in rhabdosomes about 10 mm in diameter with 40 or so preserved peripheral stipes. Autothecae appear to be simple non-denticulate tubes spaced at approximately 20 in 10 mm: near the autothecal apertures the periderm is thin. At branching points the axil is sometimes infilled with the thin-walled autotheca terminating the preceding stipe. No bithecae have been seen. The origin is unclear but may consist of a small holdfast or a very short, twisted stem.

Remarks. *Callograptus rigbyae* resembles none of the *Callograptus* species discussed under the previous description. The obvious lack of a conspicuous stem region distinguishes it from *C. bridgecreekensis* n.sp. There is a presumed superficial resemblance with the Early Ordovician *Staurograptus*, which is a siculate, planktic genus. There is also some similarity between *C. rigbyae* and *Dictyonema* sp. A of Rickards & Wright (1997) from the late Ludlow near Mumbil, NSW, but the latter has well-developed dissepiments.

Callograptus ulahensis n.sp.

Figs. 16A, 17A

Material. HOLOTYPE AM F114760 and PARATYPE AM F114780, both from BF15, S of junction of Four Mile Creek and Bridge Creek.

Derivation of name. After Ulah property.

Diagnosis. *Callograptus* with fan-like stipe clusters, connected by uncommon, hair-like dissepiments; branching in rough zones resulting in slender parallel stipes; and very simple autothecae spaced at 20 in 10 mm.

Description. Both specimens exhibit rather slender stipes 0.20–0.30 mm in lateral width and 0.40–0.50 mm in dorsoventral width. The autothecal apertures are simple, non-denticulate, spaced at 20 in 10 mm and the apertures

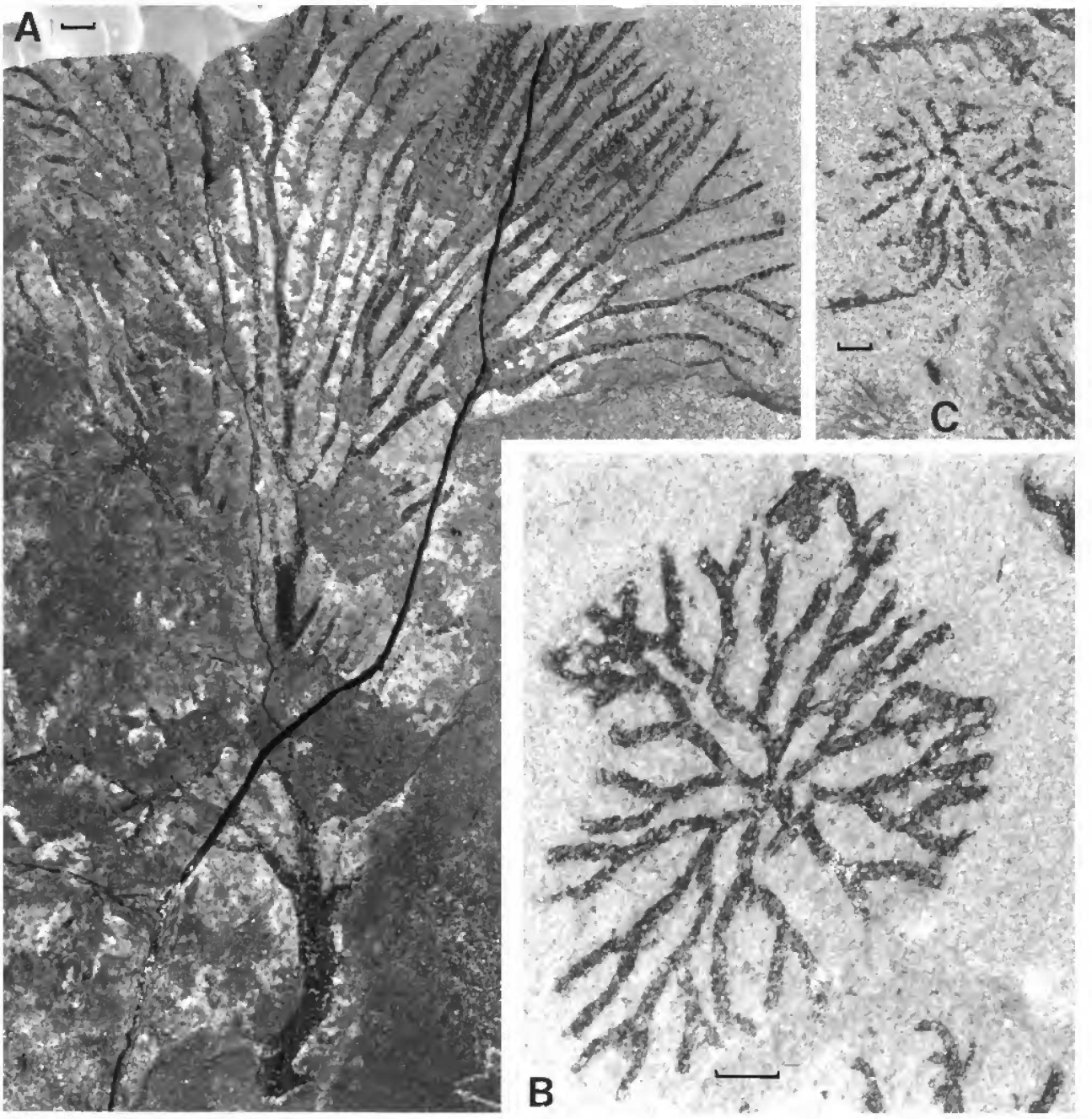

Fig. 14. *A*, *Callograptus bridgecreekensis* n.sp., AM F114569a, holotype, F14; *B,C*, *Callograptus rigbyi* n.sp., respectively AM F114651a, holotype, BF28, and paratype AM F114643, W885. Scale bars 1 mm. Note that in Fig. 14B the isolated autothecae of *Cyclograptus? australis* can be seen at bottom right and on Fig. 14C a specimen of *Acanthograptus praedeckeri* occurs at the top.

themselves occupy almost half of the dorsoventral width. The larger specimen (Fig. 16A) suggests broad branching zones. The stipes are connected by irregular and uncommon hair-like dissepiments which may be more common in the regions of the branching zones. No bithecae have been detected.

Remarks. This very simple and slender-stiped *Callograptus* bears no resemblance to any of the Silurian callograptids reviewed under the Remarks section above of the description of *C. bridgecreekensis. Callograptus ulahensis* has a different branching pattern to *C. bridgecreekensis* and a much wider thecal spacing (20 in 10 mm compared with 30–35 in 10 mm).

Callograptus cf. *niagarensis* Spencer, 1878

Fig. 16B

cf. 1878 *Callograptus niagarensis* Spencer, pp. 458, 463.
cf. 1909 *Callograptus niagarensis* Spencer; Bassler, p. 13–14, fig. 15. (A full synonymy was given by Bassler [1909]).

Material. AM F114739 from F14, Bridge Creek.

Description. A single rhabdosome with the proximal region missing shows a series of diverging, wavy stipes, probably compound to judge from the striations along their length, unconnected by dissepiments and branching in an irregular manner. The stipes are rather broad proximally, about 0.50

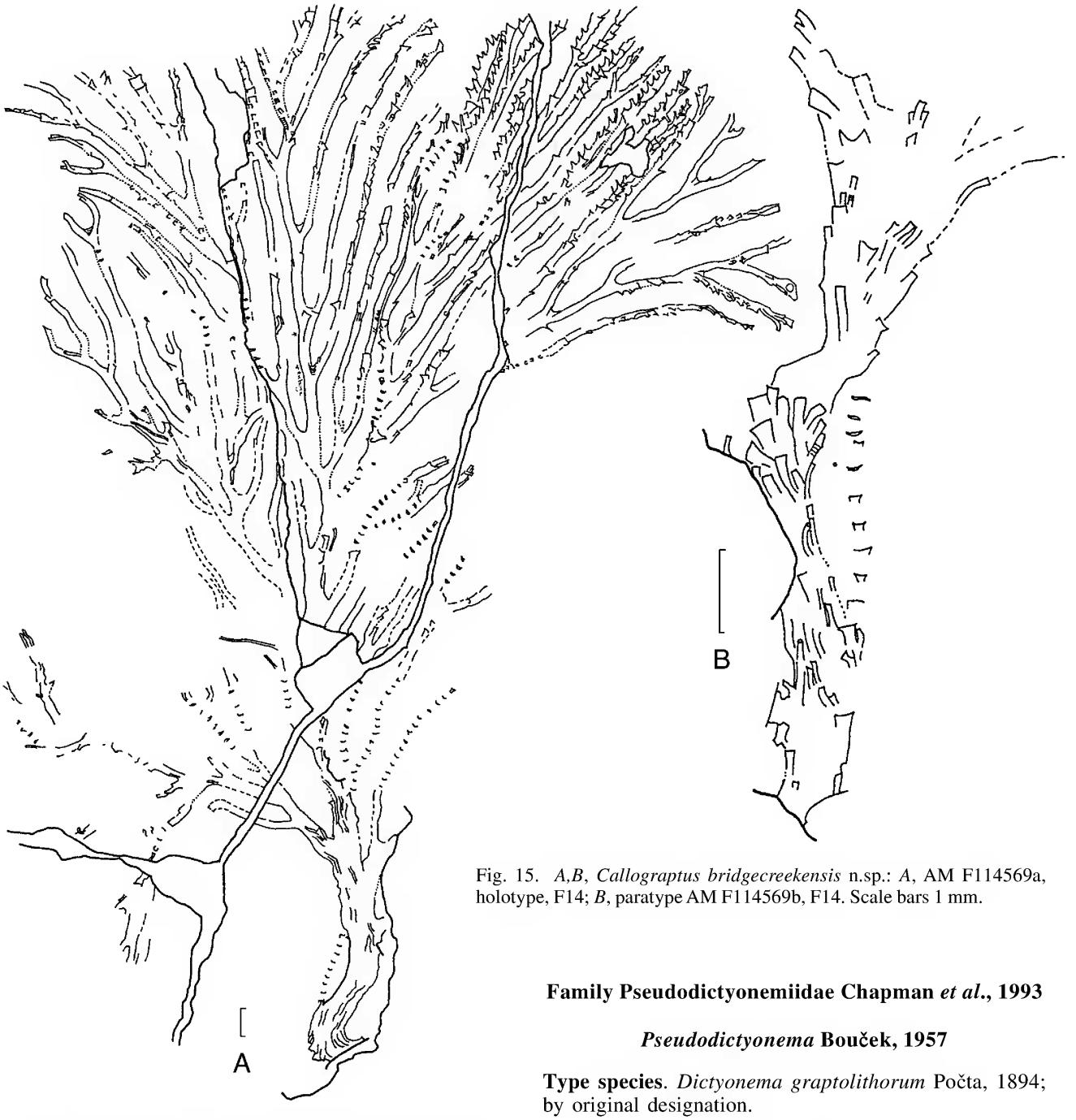

Fig. 15. *A,B*, *Callograptus bridgecreekensis* n.sp.: *A*, AM F114569a, holotype, F14; *B*, paratype AM F114569b, F14. Scale bars 1 mm.

mm, and more distally narrow to 0.25 mm, and appear to be constructed of long narrow tubes although the distal terminations of these tubes—the apertures—are not seen. Autothecae may be simple, denticulate spaced at ?20 in 10 mm.

Remarks. *Callograptus niagarensis* is known from only one specimen from the Niagaran dolomites and shales. The holotype appears to have a central dominant stipe: unfortunately this cannot be ascertained in our specimen. The wavy and diverging nature of the stipes is very similar in both specimens, but the Bridge Creek specimen has stipes which are a little more robust. Like the holotype, the Bridge Creek specimen shows bundles of tubes comprising the stipe, though not clearly. The original description suggests about 16 (auto)thecae in 10 mm (40 to the inch) which is not too different from our specimen which might be of the order of 20 in 10 mm.

Family Pseudodictyonemiidae Chapman *et al.*, 1993

Pseudodictyonema Bouček, 1957

Type species. *Dictyonema graptolithorum* Počta, 1894; by original designation.

Pseudodictyonema graptolithorum (Počta, 1894)

Fig. 16C–E

1894 *Dictyonema graptolithorum* n.sp.; Počta, p. 196, pl. 9, fig. 14.
1957 *Dictyonema (Pseudodictyonema) graptolithorum* Počta, 1894; Bouček, p. 69–70, pl. 7, pl. 8, figs. 4–6, text-fig. 27a–c.

Material. AM F114753, AM F114755 and AM F114645, all from F14, Bridge Creek.

Diagnosis. *Pseudodictyonema* with characteristically ropy, compound stipes, a rectangular meshwork defined by stipes and robust dissepiments; stipes spaced at 14–16 in 10 mm; dissepiments 8–13 in 10 mm; stipes 0.30–0.50 mm wide; autothecal spacing about 14–15 in 10 mm.

Description. The stipes are markedly parallel and the meshwork strikingly rectangular. The largest rhabdosome in our collection is 15 mm long by 25 mm wide, probably developed from a short stem. The autothecae have isolated apertural regions at the ends of long tubes which, with numerous others, make up the ropy texture of the stipes. Despite the obvious complexity of the stipes the autothecal apertures are spaced regularly at 14–15 in 10 mm. Dissepiments vary from very fine to quite robust and it is likely that some involve transfer of the thecal tubes from one stipe to the next. The spacing is also variable but in the range 8–13 in 10 mm. One specimen, AM F114645, has dissepiments spaced as high as 12–13 in 10 mm in places.

Remarks. The only difference between our material and the Czech types is that the types have a higher dissepimental spacing (15–16 in 10 mm given by Bouček, 1957); his figures 27a and 27c have much lower dissepimental spacing than given in his text (actually 5–6 in 10 mm).

Family Stelechocladiidae Chapman *et al.*, 1993

Stelechocladia Počta, 1894

Type species. *Stelechocladia subfruticosa* Počta, 1894, subsequently designated by Bouček (1957).

Stelechocladia praeattenuata n.sp.

Figs. 17B, 19A,B

Material. HOLOTYPE AM F114743a-b, from BF28, W tributary of Bridge Creek. PARATYPES AM F114765 from BF14, Bridge Creek; AM F114781 from F14, Bridge Creek; AM F114782a-b from BF18; AM F114783 from F19, Four Mile Creek; and AM F114784 from BF18.

Derivation of name. To reflect its earlier occurrence than the most similar species, *Stelechocladia attenuata* Bouček, 1957.

Diagnosis. Robust *Stelechocladia* with dominant main stipes and shorter, intermediate, finer stipes quite regularly arranged; 10–14 stipes in 10 mm; autothecal spacing 30–40 in 10 mm; rhabdosome developed from broad holdfast; stipes with proximal lateral width of 1.0 mm at most; dorsoventral width 0.70–0.90 mm.

Description. The rhabdosome develops from a holdfast 3–5 mm across; although detailed growth close to the holdfast is not clear, three or four main stipes seemingly arising from an amorphous mass of tissue. The mains stipes are initially up to 1 mm wide (lateral width) though usually less than this. More distally they gradually become narrower reaching 0.25–0.30 mm. Intermediate stipes are similarly tapered. However, when seen in profile view, when the denticulate autothecae are clearly visible, the dorsoventral width is fairly constant at 0.70–0.90 mm. Branching from the main stipes is frequent but irregular, and it tends to be from one side of the main stipe. Branching from the main stipes takes place every 0.50–1.50 mm. The result of the branching is a striking array of spike-like stipes, quite unconnected (except at the branching points) with shorter, intermediate stipes filling the spaces between main stipes. Many intermediate stipes are rather short and seem to be positioned merely to fill a space between two adjacent but distally converging longer stipes. No bithecae have been detected.

Remarks. *Stelechocladia attenuata* from the Přídolí of the Czech Republic is undoubtedly the closest species but is much larger and altogether more robust than in *S. praeattenuata*, and also has a wider autothecal spacing (25 in 10 mm compared with 30–40 in 10 mm: see Kraft, 1984).

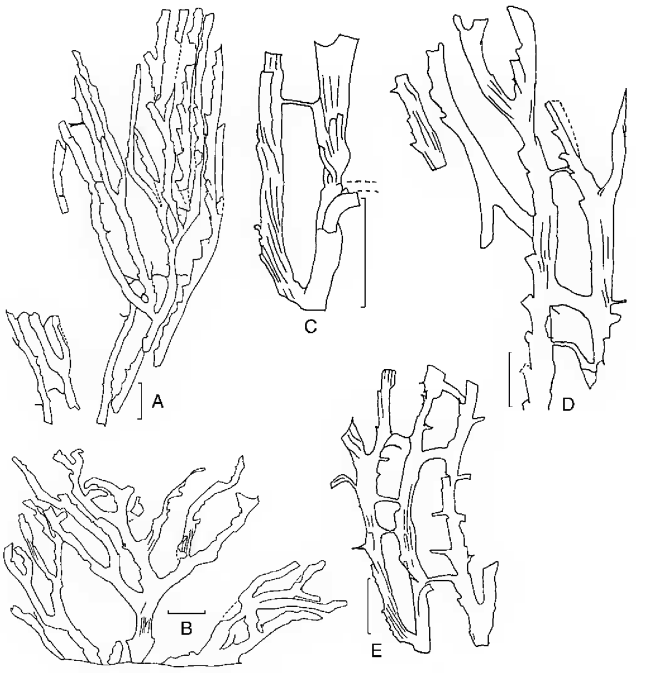

Fig. 16. *A*, *Callograptus ulahensis* n.sp., AM F114760, holotype, BF15; *B*, *Callograptus niagarensis*, AM F114739, W885; *C–E*, *Pseudodictyonema graptolithorum*, respectively AM F114755, AM F114753 and AM F114645, all from F14. Scale bars 1 mm.

Family Acanthograptidae Bulman, 1938

Acanthograptus Spencer, 1878

Type species. *Acanthograptus granti* Spencer, 1878; by original designation.

Acanthograptus praedeckeri n.sp.

Figs. 17C,D, 18A, 19C, 20A–E

Material. HOLOTYPE AM F114792a-b, from BF28, Bridge Creek. PARATYPES AM F114629a, AM F114718, AM F114740a-b, AM F114741, AM F114785–89 and AM F114791, all from F14; AM F114742 from BF29, W tributary of Bridge Creek; AM F114630 from F6, Wallace Creek; AM F114568a-b, AM F114741, AM F114790–1 and AM F114793–4, all from BF28, W tributary of Bridge Creek.

Derivation of name. To reflect its earlier occurrence than the low Ludlow species *A. deckeri*, which it resembles.

Diagnosis. Large, flabelliform *Acanthograptus* in which the main stipes grow from a robust stem region; twigs and

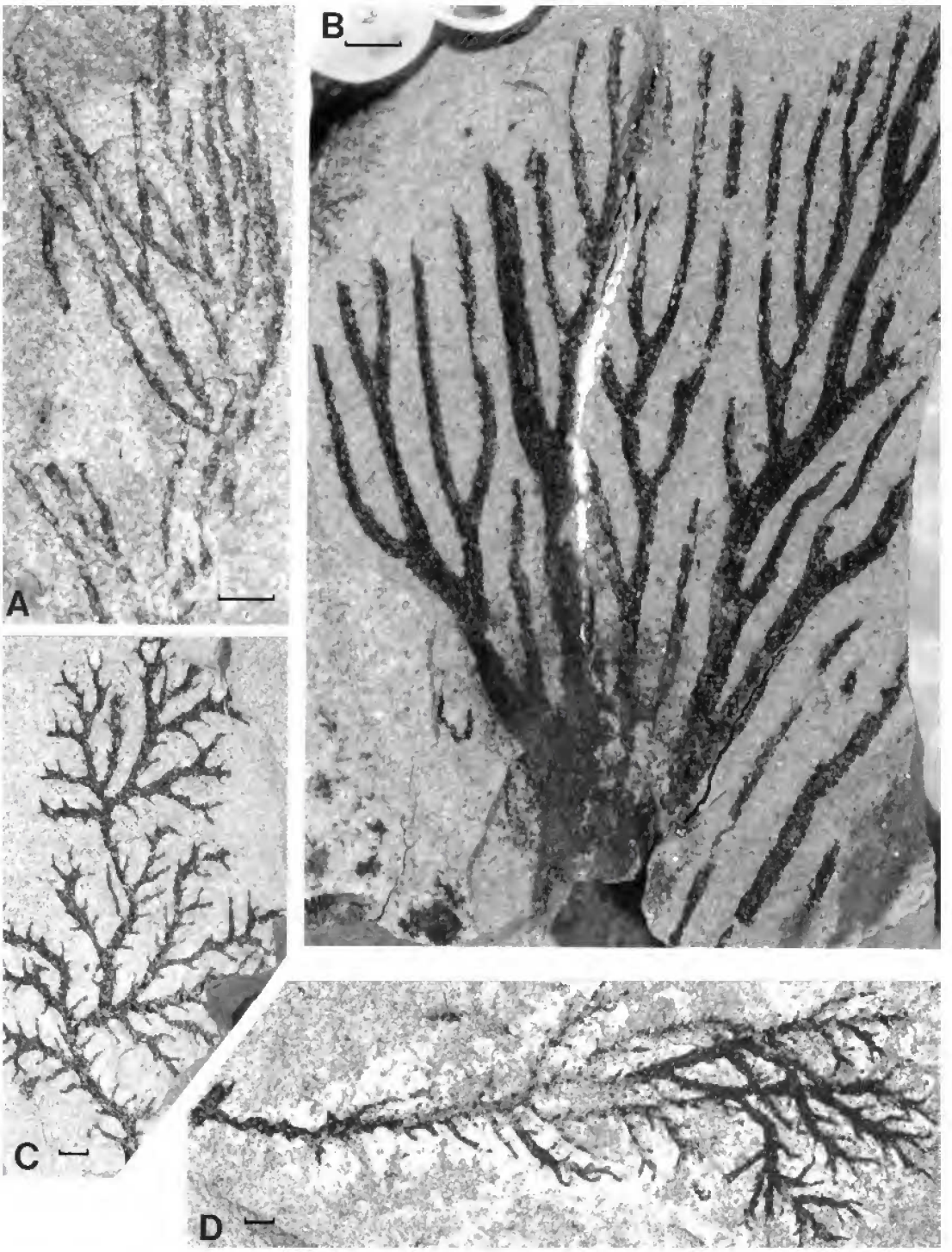

Fig. 17. *A*, *Callograptus ulahensis* n.sp., AM F114760, holotype, BF15; *B*, *Stelechocladia praeattenuata* n.sp., AM F114743, holotype, BF28; *C,D*, *Acanthograptus praedeckeri praedeckeri* n.sp., respectively AM F114792, holotype, BF28 and AM F114568a, F14. Scale bars 1 mm.

secondary branches spread to all available space; 8–14 twigs in 10 mm; twigs 0.70–1.0 mm long; main stipe 0.40–0.50 mm wide; branching every 0.50–1.50 mm.

Description. In the best preserved specimens there is no physical overlap of adjacent stipes. Rather, the overall branching pattern grows and spreads in all directions to fill the available space. Thus the rhabdosome, although bush-like in appearance, is actually flabelliform. In sections of stipe where no branching takes place the twigs alternate from side to side in classic *Acanthograptus* fashion. Each twig usually comprises more than one autothecal tube although some seem to terminate in a single tube. However, the twig arrangement breaks down frequently because numerous dichotomies of the stipes occur, spaced at 0.50–1.50 mm intervals. All the stipes appear to be compound with numerous elongate tubes visible.

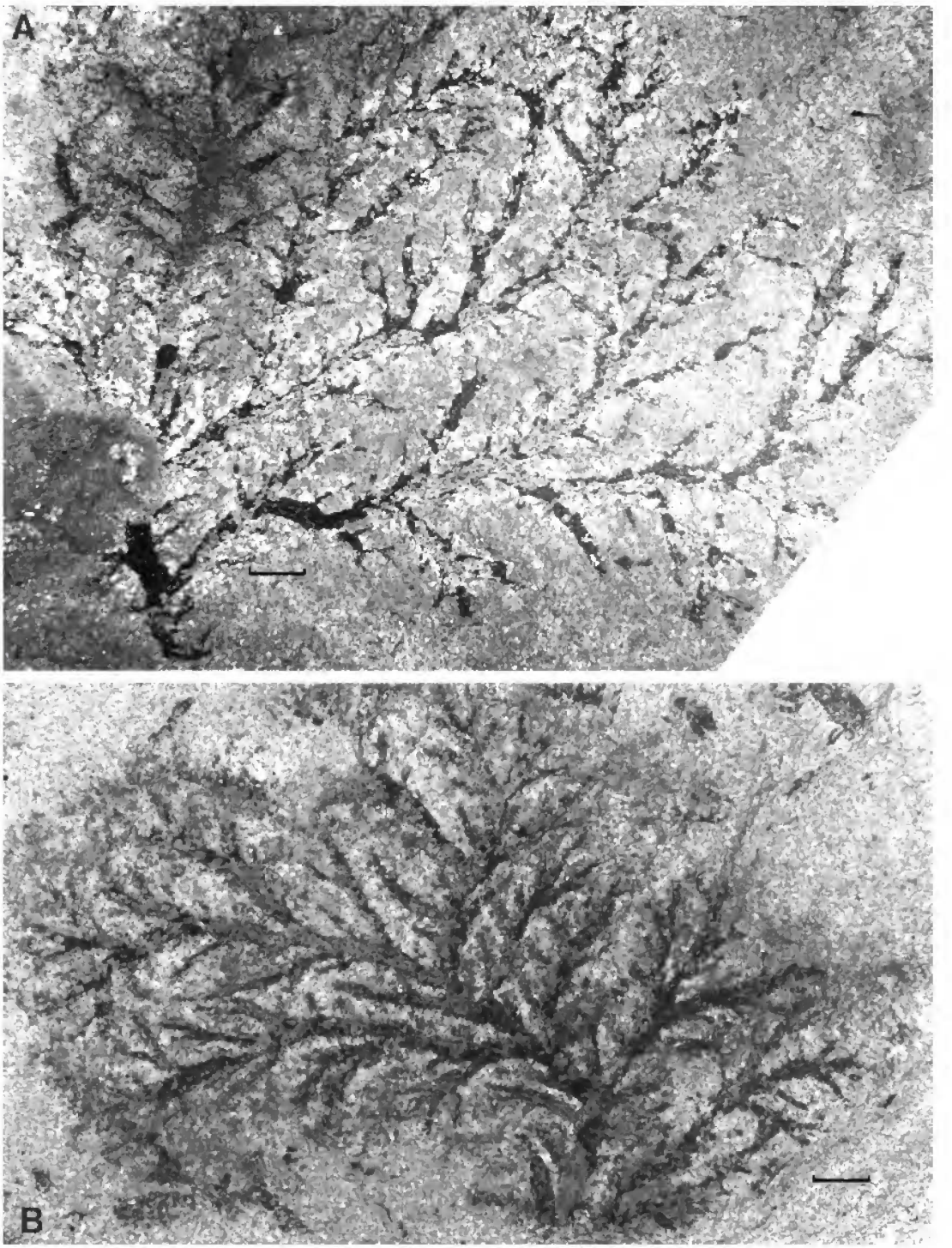

Fig. 18. *A*, *Dictyonema warrisi* n.sp., AM F114629b, F14; *B*, *Thallograptus christoffersonae* n.sp., AM F114644, W885. Scale bars 1 mm.

Remarks. *Acanthograptus praedeckeri* n.sp. has too few twigs and too great a stipe width for comparison with *A. aculeatus* Počta, as well as having a bushier rhabdosome altogether. *Acanthograptus deckeri* from the low Ludlow has a similar rhabdosomal appearance, but the twig arrangement is less regular and all the stipes more compound and more robust. *Acanthograptus praedeckeri* is very similar to *Thallograptus christoffersonae* described below, and the differences are listed under the Remarks section of the latter.

***Acanthograptus praedeckeri minimus* n.subsp.**

Fig. 20F

Holotype. AM F114630, from F6, Wallace Creek.

Derivation of name. To indicate smaller dimensions than the nominate subspecies.

Diagnosis. *Acanthograptus praedeckeri* differing from the nominate subspecies in: its much smaller form with narrower stipes, the more open "space coverage" by the branching, and with twig spacing twice as frequent.

Description. The single well-preserved rhabdosome shows several well-developed branches and numbers of twigs. The stipes are uniformly narrow at 0.20 mm yet clearly compound with bundles of long narrow tubes. It is possible that some of the twigs may terminate with a single autotheca but parts of some twigs have more than one thecal tube involved. Some thecae appear to open on the main stipes, their apertures adpressed to the surface. Twigs are 0.30–0.60 mm long, usually directed at about 45° to the stipe axis; twig spacing more than 20 in 10 mm.

Remarks. Although having the same general appearance as the type subspecies, *A. p. minimus* is a much smaller form with narrower stipes and the "space coverage" by the branching is more open. It is difficult to give a twig spacing accurately, because of the numbers of branches, but twig spacing is certainly twice as frequent as in the type subspecies.

Thallograptus Ruedemann, 1925

Type species. *Dendrograptus? succulentus* Ruedemann, 1905, by original designation.

Thallograptus christoffersonae n.sp.

Figs. 18B, 22A,B

Material. HOLOTYPE AM F114746, W885 (approximately = BF14 and F14), Bridge Creek. PARATYPES AM F114644, W885 and AM F114765, BF14; and numerous other specimens from F14, BF24, BF28, and BF29, all uppermost Llandovery.

Derivation of name. After Ruth Christofferson of "Avon Lea".

Diagnosis. *Thallograptus* with very bushy dendroid appearance, fan-shaped; stipes no more than 0.60 mm wide, branching every 1 mm or less; about 10 stipes per cm; twigs at rate of 12 per cm, up to 1 mm long, terminating as one autothecal tube; autothecae 0.10–0.15 mm wide; bithecae 0.03–0.04 mm wide.

Description. The rhabdosome, measuring up to 25 mm wide and 15 mm long on the largest specimens, is probably fan-shaped because despite the dendroid, fan-shaped appearance stipes do not overlap but fill the available space. A holdfast has not been identified. At their thickest the stipes are about 0.60 mm wide, and branching takes place regularly, usually with intervals of less than 1 mm between branches. Branches diverge in such a manner that the available space is filled. There is no anastomosis. Twigs occur between branching points and are spaced at around 10–12 per cm with an individual length of up to 1 mm. They terminate in single autothecal tubes having a diameter of 0.10–0.15 mm and unornamented apertures. Along the main stipes bundles of up to 6 autothecae are visible in the ropy stipe texture, implying that there are considerably more in any one cross section of stipe. Bithecae are seen occasionally as diminutive tubes, 0.03–0.04 mm wide, irregularly positioned.

Remarks. The closest species seems to be *T. elegans* Bouček, 1957, which has a similar growth pattern of the stipes. In this form, however, the stipes are much thicker, and they thin and thicken at branching points which does not occur

Fig. 19. *A,B, Stelechocladia praeattenuata* n.sp.: *A*, AM F114743, holotype, and *B*, AM F114744, both BF18; *C*, *Acanthograptus praedeckeri praedeckeri* n.sp., AM F114629a, F14. Scale bars 1 mm.

Fig. 20. *A–E*, *Acanthograptus praedeckeri praedeckeri* n.subsp., respectively AM F114568, AM F114568, AM F114741, AM F114742 and AM F114740, all from F14; *F*, *Acanthograptus praedeckeri minimus* n.subsp., AM F114630, F6. Scale bars 1 mm.

in *T. christoffersonae*. Other measurements, such as stipe spacing and branching frequency, also differ. *Acanthograptus praedeckeri* n.sp. is also similar in rhabdosomal form (and it is interesting that Bouček (1957: 102) referred his new species *A. deckeri* inadvertently to *Thallograptus*!). *Acanthograptus praedeckeri* n.sp. differs from *Thallograptus christoffersonae* n.sp. in having a definite twig system where each twig is composed of several thecae, the twigs are shorter, and branching is much less frequent. *Thallograptus densus* Kraft, 1979 is another similar species but differs in having more parallel and more densely arranged stipes; it occurs in the *sedgwickii* Biozone (Llandovery). *Thallograptus elegans* is a Wenlock to Ludlow species.

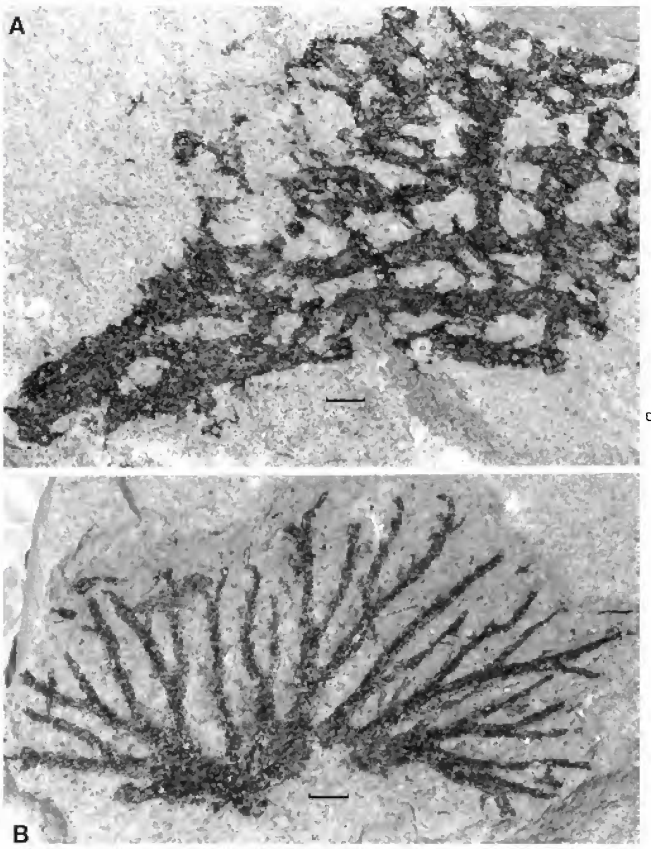

Fig. 21. *A*, *Koremagraptus obscurus* n.sp., AM F114745, holotype, BF28; *B*, *Cyclograptus? australis* n.sp., AM F114651, holotype, BF28. Scale bars 1 mm.

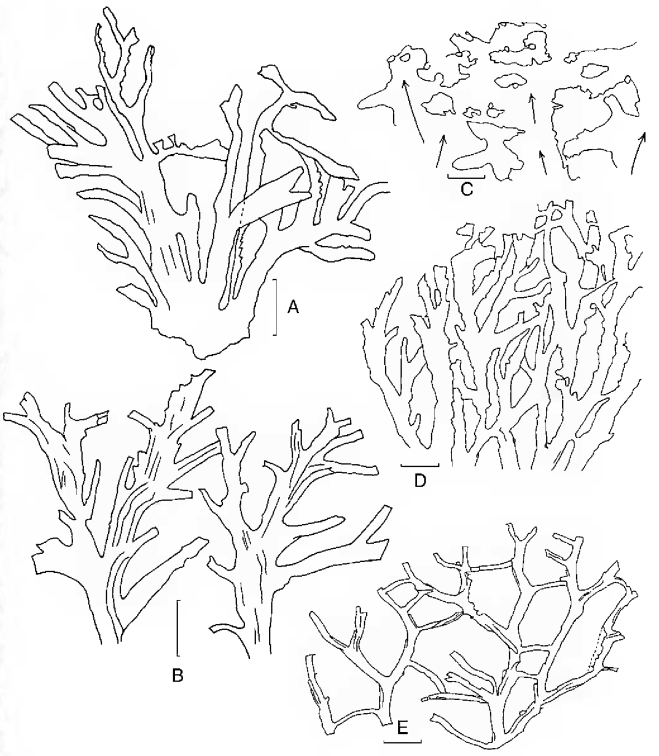

Fig. 22. *A,B. Thallograptus christoffersonae* n.sp.: *A*, AM F114765, stipe development from basal holdfast, BF14 and *B*, AM F114746, holotype, F14; *C*, *Koremagraptus obscurus* n.sp. AM F114745, holotype, BF28; *D*, *Koremagraptus elegantulus* n.sp. AM F114752, holotype, W885; *E*, *Reticulograptus thomasi* n.sp. AM F114756, holotype, BF28. Scale bars 1 mm.

Koremagraptus Bulman, 1927

Type species. *Koremagraptus onniensis* Bulman, 1927, by original designation

Koremagraptus obscurus n.sp.

Figs. 21A, 22C

Material. HOLOTYPE AM F114745, the only specimen, from BF28, W tributary of Bridge Creek.

Diagnosis. *Koremagraptus* with growth direction of individual stipes difficult to ascertain due to complex and rapid anastomosis; most thecal apertures, with a diameter of 0.15 mm, are located on stipe walls and only rarely isolated.

Derivation of name. Reflecting the complex anastomosis of stipes.

Description. The large fragment of rhabdosome exhibits a complex mass of anastomosing stipes. Each stipe is clearly composed of numerous thecal tubes. Most thecal apertures are located on the stipe walls and only rarely are isolated. In Fig. 22C the arrows indicate the growth directions of three stipes. It is immediately obvious that in a distance of only 3 mm several instances of complex anastomosis occur. Most anastomosis seems to involve the transfer from one stipe to another of whole bundles of tubes. The tube apertures—presumed autothecal apertures—have a diameter of 0.15 mm. There is a suggestion that the stipes and thecal tubes are thin walled.

Remarks. *Koremagraptus obscurus* n.sp. has the characteristics of previously-described koremagraptids but taken to extremes in that the growth direction of individual stipes is difficult to ascertain at any one point, so great is the anastomosis. *Koremagraptus obscurus* can be contrasted, for example, with *K. elegantulus* n.sp., which is a more typical koremagraptid in its stipe arrangement. It is possible that other fragments in our collections might be referable to *K. obscurus* because small pieces of complex, thin-walled stipe fragments are not uncommon. *Koremagraptus flexuosus* Bouček, 1957 from the basal Devonian has a similar stipe pattern but is less densely connected.

Koremagraptus elegantulus n.sp.

Fig. 22D

Material. HOLOTYPE AM F114752 from F14, Bridge Creek and PARATYPE AM F114717a-b from W885, Bridge Creek.

Derivation of name. Reflecting the nature of the stipe pattern.

Diagnosis. *Koremagraptus* with gently diverging and anastomosing robust compound stipes 0.50–0.70 mm across; lacks recognizable autothecae.

Description. The large portion of rhabdosome measures 35 mm by 25 mm, and is typified by gently diverging and anastomosing robust stipes, each about 0.50–0.70 mm across except at points of anastomosis where they are wider. A number of twig-like terminations occur, often extending into the spaces formed by the anastomosing main stipes. Some of the "twigs" may terminate as single autothecal

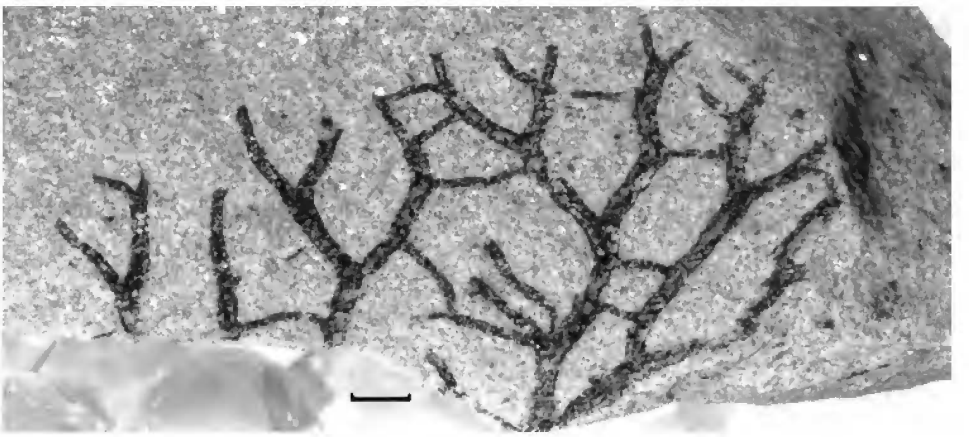

Fig. 23. *Reticulograptus thomasi* n.sp., AM F114756, holotype, BF28. Scale bar 1 mm.

tubes. Autothecae have not been readily identified, however, and no thecal spacing figure is possible. All stipes are clearly compound with bundles of elongate thecae.

Remarks. *Koremagraptus pseudoplexus* Bouček, 1957 from the Wenlock of Bohemia is one of the closest forms, having a similar pattern of stipes, but it is less robust than *K. elegantulus* and has frequent dissepiment-like branch connections which *K. elegantulus* lacks.

Order Tuboidea Kozlowski, 1938

Family Tubidendridae Kozlowski, 1949

Reticulograptus Wiman, 1901

Type species. *Dictyonema tuberosum* Wiman, 1895, by original designation.

Reticulograptus thomasi n.sp.

Figs. 22E, 23

Material. HOLOTYPE AM F114756, only specimen, from BF28, W tributary of Bridge Creek.

Derivation of name. After the late Dr D.E. Thomas, Australian biostratigrapher and graptolite authority.

Diagnosis. *Reticulograptus* with striking polygonal arrangement of stipe interspaces; only autothecae and possible bithecae have been identified, with no clustering of thecae into twigs, or even single autothecal terminations; no association of autothecae and bithecae,

Description. The only rhabdosomal fragment is exquisitely preserved with many individual autothecal tubes visible. Each stipe is effectively zig-zag and connections with adjacent stipes are exclusively transfers of autothecal tubes. Autothecal apertures are sometimes associated with the transfer from an adjacent stipe, with an autotheca opening just before or just after the point where the "arriving" theca reaches its new stipe position. Some smaller tubes may be bithecae, as at the extreme left of Fig. 22E. Autothecae and the possible bithecae open close to the stipe surface. Autothecal tubes have an average diameter of about 0.10 mm and the possible bithecae 0.05 mm. Stipe width is 0.20–0.35 mm. Stipes are compound with several elongate tubes comprising any one part of them. Branching gives an overall divergent pattern, and the interspaces are polygonal. Stipe spacing is 8 in 10 mm. Strictly speaking there are no dissepiments but the connecting bars of autothecal tubes are also spaced at about 8 in 10 mm.

Remarks. *Reticulograptus thomasi* n.sp. is a unique reticulograptid in its striking polygonal arrangement of stipe interspaces, although all the other biocharacters are typically reticulograptid. Only autothecae and possible bithecae have been identified, but there is no clustering of these into twigs, or even single autothecal terminations, and no association of autothecae and bithecae, all of which suggest this is a tuboid rather than a dendroid.

Family Idiotubidae Kozlowski, 1949

Cyclograptus Spencer, 1884

Type species. *Cyclograptus rotadentatus* Spencer, 1884, p. 42; by original designation.

Remarks. Bulman (1970) referred to the branching of stipes at their mid-length in his revised diagnosis of the genus. However, the original material is not quite so consistent as this, as pointed out by Bouček (1957) who recorded much longer stipes in some species than in the type species. In Bouček's species (*C. irregularis* and *C. multithecatus*) and *C. scharyanus* (Göppert, 1860) the stipes divide at roughly mid-length, but with additional bifurcations occurring. Bouček (1957: p. 141) also questioned whether, given such long stipes, all the autothecae must originate in the thecorhiza: it seems unlikely.

Cyclograptus? australis n.sp.

Fig. 21B

Material. HOLOTYPE AM F114651, from BF28, Bridge Creek.

Derivation of name. To record the possible occurrence of the genus in Australia.

Diagnosis. *Cyclograptus*? with thecorhiza; 32 peripheral stipes some 6 mm from thecorhiza; autothecal apertural regions clearly isolated; autothecal diameter 0.15 mm and spacing approximately 18–20 in 10 mm; bithecae possibly present as thin tubes in thecorhiza.

Description. The single rhabdosome has a "basal disc" or thecorhiza 7 mm wide, possibly incomplete, from which about ten stipes arise. These bifurcate quite quickly, and then divide again in some cases, resulting in 32 peripheral

stipes some 6 mm from the thecorhiza. The rhabdosome appears to be incomplete although its general shape is clear. The stipes consist of bundles of long thecal tubes, and in several places the autothecae can be seen opening in isolated fashion, sometimes slightly bent ventrally. Their diameter is 0.15 mm and the autothecal spacing approximately 18–20 in 10 mm. The autothecal apertures appear to be unadorned by processes or spines except, possibly, a slight extension of the ventral lip. Long thecal tubes can be detected in both the thecorhiza and in the up-growing stipes, but the termination of the stipes is usually by a single ventrally-curved autotheca. Bithecae may be present as thin tubes in the thecorhiza but this is not certain. The stipes may be unbranched, may branch after one third of their length, occasionally after two thirds of their length, and two stipes branch three times.

Remarks. The thecae are unknown in any described species of *Cyclograptus*, other than as bundles of elongate tubes in the thecorhiza and stipe. In *C.? australis* n.sp. the autothecal apertural regions are clearly isolated. The type species, *C. rotadentatus*, also exhibits stipes terminating in a single autotheca, but is more regular in its branching than *C.? australis*. *Cyclograptus scharyanus* (Göppert, 1860) has a stem-like structure, unlike other cyclograptids. *Cyclograptus irregularis* Bouček, 1957 is a much more robust species with broad stipes, and *C. multithecatus* Bouček, 1957 has more compound stipes than *C.? australis*. All previously described species of *Cyclograptus* are Wenlock (Silurian) whereas our specimen is late Llandovery. The presence of a thecorhiza in *C.? australis* with masses of thecal tubes, suggest the tuboid *Cyclograptus* but the stipe branching pattern seems greater than in other cyclograptids except perhaps *C. multithecatus*.

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